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Reversing Tree Encroachment Increases Usable Space for Sage-Grouse during the Breeding Season

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ABSTRACT

In the Great Basin, coniferous trees are expanding their range at a rate higher than any other time during the Holocene. Approximately 90% of the expansion has occurred in ecosystems previously dominated by sagebrush (*Artemisia* spp.). Transitions from open, sagebrush steppe to woodlands are considered a threat to the greater sage-grouse (*Centrocercus urophasianus*), a sagebrush obligate gallinaceous bird that occupies approximately 56% of its pre-European settlement distribution. Using a telemetry data set from 2010–2017 breeding seasons for a treatment area with conifer removal and an experimental control area, we assessed the efficacy of conifer removal for increasing usable space and determined relative probability of use of a landscape previously impacted by conifer expansion. Sage-grouse increasingly selected areas closer to conifer removals and were 26% more likely to use removal areas each year after removal. Sage-grouse were most likely to select areas where conifer cover had been reduced by ≤10%. The proportion of available locations having a high relative probability of use increased from 5% to 31% between 2011 and 2017 in the treatment area and locations with the lowest relative probability of use decreased from 57% to 21% over the same period. Dynamics in relative probability of use at available locations in the control area were stochastic or stable and did not demonstrate clear temporal trends relative to the treatment area. Targeted conifer removal is an effective tool for increasing usable space for sage-grouse during the breeding season and for restoring landscapes affected by conifer expansion.

The expansion of native, woody plants into shrub and grassland ecosystems resulting from changes in fire regimes, land use patterns, climate, and CO_2 concentrations is a global phenomenon and vexing ecological problem (Miller and Wigand 1994, Staver et al. 2011, Nackley et al. 2017). In the Great Basin of western North America, a native coniferous tree, western juniper (*Juniperus occidentalis*), has expanded its range tenfold since European settlement and at a rate higher than any other time during the Holocene (Miller and Wigand 1994, Miller et al. 1999). Approximately 90% of the expansion since European settlement has occurred in sagebrush (*Artemisia* spp.) ecosystems (Miller et al. 2005, Miller et al. 2011). More broadly, it is estimated that nearly 500,000 km^2 of the sagebrush ecosystem have been encroached by coniferous trees (Falkowksi et al. 2017).

The impact of conifer expansion in North America is not unique to sagebrush ecosystems and extends to other grassland and shrubland habitats. Conifer cover is an influential predictor of greater prairie-chicken (*Tympanuchus cupido*) lek (i.e., breeding arena) presence (Merrill et al. 1999, Niemuth 2003), and one study found 9% conifer cover as a threshold to suitability of prairie habitat for lek sites (Gregory et al. 2011). In addition to influencing probability of lek occurrence and occupancy, increased conifer cover is associated with lower probability of nesting and reduced nest survival (Matthews et al. 2013, Hovick et al. 2015). Lesser prairie-chickens (*T. pallidicinctus*) avoid conifers and other trees year-round and select nest sites in areas with low tree densities (Boggie et al. 2017, Lautenbach et al. 2017). Lesser prairie-chicken lek occupancy is unlikely when cover of conifers exceeds 2.8% within 500 m of lek sites (Hagen et al. 2019).

The greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse), a ground-dwelling sagebrush obligate bird, has declined 0.83% per year range-wide since 1965 (WAFWA 2015). It occupies approximately 56% of its pre-European settlement distribution (Schroeder et al. 2004). Expansion of western juniper and other conifers into sagebrush ecosystems is considered a threat to sage-grouse habitat, particularly in the Great Basin, and has likely contributed to reductions in sage-grouse distribution (Miller et al. 2011, Baruch-Mordo et al. 2013, Doherty et al. 2018, Reinhardt et al. 2020). Radio telemetry studies indicate that sage-grouse are more likely to select sagebrush habitats with conifer cover levels ≤4%, and as low as 1.5%, indicating a low tolerance for conifers even in areas with intact sagebrush understories (Coates et al. 2017, Severson et al. 2017*a*). Sage-grouse vital rates are generally negatively affected by the presence of conifers in sage-grouse habitat (Coates et al. 2017, Sandford et al. 2017, Olsen et al. 2021), and sage-grouse navigating landscapes affected by conifer expansion move more quickly and have increased predation risk, particularly among juveniles (Prochazka et al. 2017).

During the breeding season, sage-grouse occupy habitats critical to nesting/early brood and late brood-summer life history needs (Connelly et al. 2011). Given the negative effects of conifer cover on sage-grouse habitat selection, conifer expansion may reduce the amount of usable space (Guthery 1997) in important habitats as sage-grouse are functionally excluded as tree density and extent expands. Although the usable space hypothesis is largely applied to northern bobwhite (*Colinus virginianus*) management, it may have applicability to the sage-grouse. Applying this concept to sagebrush habitat affected by conifer expansion and with largely intact understory vegetation, the quality of habitat can be expressed as the proportion that is fully usable to sage-grouse (Guthery 1997). The usable space hypothesis emphasizes habitat quantity, which coincides with the conclusions of a recent range-wide assessment of sage-grouse nesting habitat (Smith et al. 2020). However, quality, connectivity, and other habitat components of sage-grouse habitat are important considerations for effective management in space and time. Conifer removal near nesting and summer habitats or along seasonal migration routes from early to late brood habitat may increase usable space for sage-grouse (Sandford et al. 2017, Reinhardt et al. 2020). Brood habitat limits the carrying capacity of sage-grouse, and loss of brood habitat is considered a major factor in the decline of sage-grouse populations (Donnelly et al. 2016).

Our study expanded previous resource selection analyses (Severson et al. 2017*a*, 2017*b*) for sage-grouse in a treatment area (area with conifer removal; hereafter Treatment) and a control area (area without conifer removal; hereafter Control). Previous analyses assessed the short-term (1–3 years post-removal) response of sage-grouse habitat selection to conifer presence and conifer removal (Severson et al. 2017*a*, 2017*b*). Building on the original data set, our study assessed the longer-term response (3–7 years post-removal) of breeding-season habitat selection by sage-grouse to conifer presence and removal. The broader temporal scale of the data set served to validate and refine previous results and management recommendations while accounting for inter-annual variation in habitat characteristics and selection probabilities. Additionally, we incorporated location data from GPS technology at greater temporal resolution and sample size to improve parameter estimation. Our objective was to assess the influence of conifers and habitat restoration with conifer removal on sage-grouse habitat selection during the breeding season. Finally, we sought to assess temporal and spatial landscape dynamics in predicted probability of use of sage-grouse habitat as a result of conifer removal.

STUDY AREA

The majority of our study area was in Lake County, Oregon, USA, within the Lakeview District of the Bureau of Land Management (BLM) Resource Area (Fig. 1). The Treatment encompassed approximately 40,000 ha and occurred entirely in Lake County, Oregon. The Control encompassed approximately 33,000 ha and extended south into Washoe County, Nevada and Modoc County, California, USA. Average elevation was 1,700 m and ranged from 1,200 to 2,200 m. Most of the study area was dominated by uplands characterized by Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), mountain big sagebrush (*A. tridentata* ssp. *vaseyana*), and bunchgrass (Poaceae) plant associations. Mesic resources indicative of sage-grouse summer habitat such as wet meadows, irrigated fields, riparian areas, and high elevation habitats with higher soil moisture content were also available in the study area.

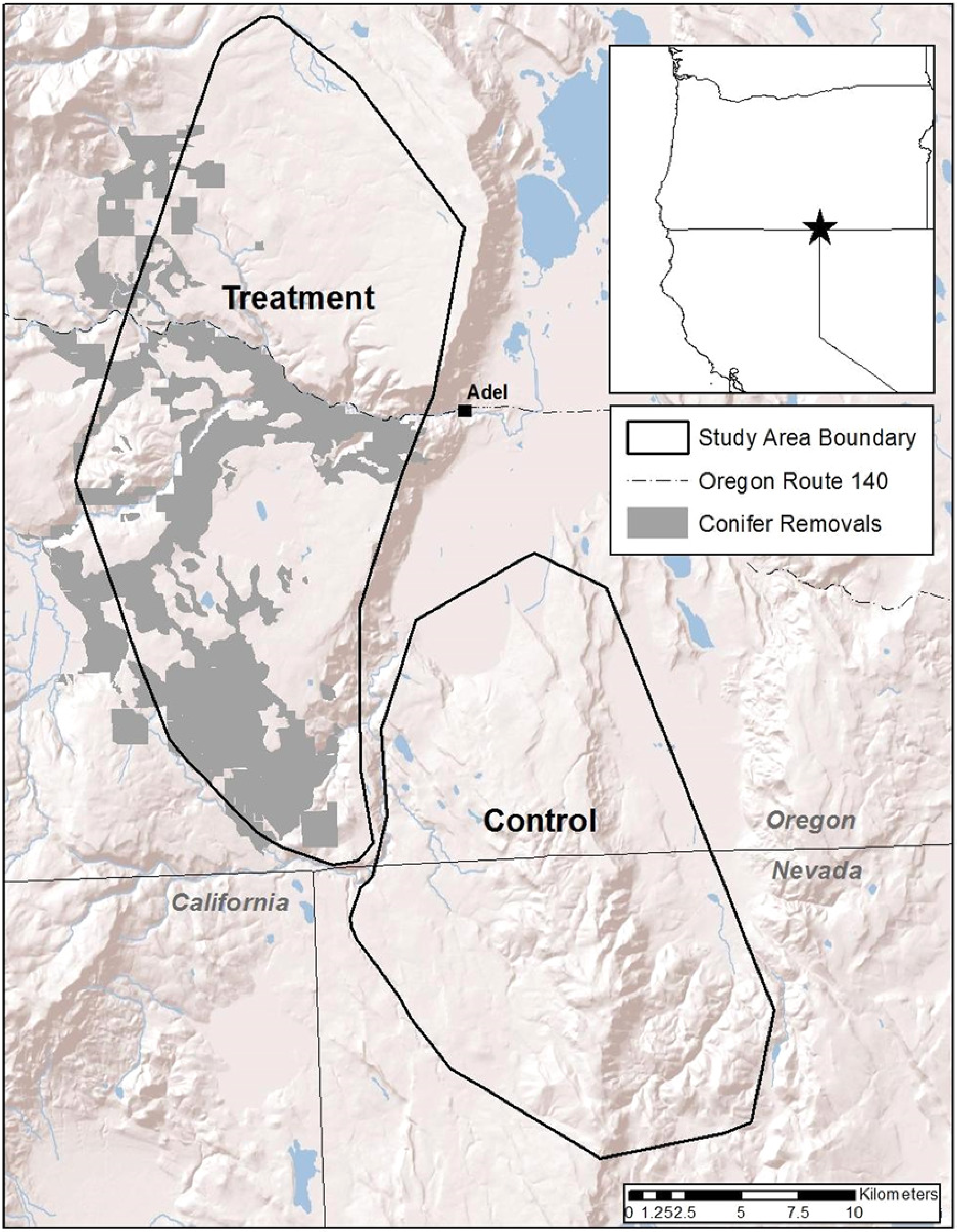

Figure 1

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Treatment and control study areas for research on sage-grouse habitat use in relation to conifer removals, 2010–2017, Lake County, Oregon and Washoe County, Nevada, USA.

Conifer woodlands comprised predominantly of western juniper covered approximately 43% (17,000 ha) of the Treatment prior to removal. Following the transitional phases described by Miller et al. (2005), the woodlands in the Treatment were comprised of approximately 3,000 ha Phase I, 12,000 ha Phase II, and 2,000 ha Phase III (BLM 2011). Phase I woodlands had trees present but shrubs and herbaceous plants were the dominant vegetation influencing ecological function, Phase II woodlands were co-dominated by trees, shrubs, and herbaceous plants, and Phase III woodlands were dominated by trees (Miller et al. 2005). The BLM initiated removal of approximately 9,983 ha of conifers in the Treatment in 2012, consisting of 1,566 ha Phase I, 7,864 ha Phase II, and 553 ha Phase III woodlands (Table 1). Additionally, the U.S. Department of Agriculture's Natural Resources Conservation Service (NRCS) in partnership with agricultural producers completed approximately 3,683 ha of removals on private lands within the study area. Most removals were completed by the end of 2014 and all remaining removals were completed by 2017 (Table 1). Hand cutting was the primary removal technique used, which minimized disturbance to understory vegetation and invasion of invasive annual grasses (BLM 2011). Where trees were sparse, they were felled, and limbs were scattered to minimize slash height (BLM 2011). When fire was used to remove slash, effort was made to limit the effect of fire to slash piles for individual trees and their stumps (i.e., pile burning) and burning took place during winter and early spring months when risk of fire spreading to nontarget fuels was minimal. Conifers that established prior to European settlement were not removed (BLM 2011).

Table 1. Annual and cumulative area of conifers removed on public and private lands in a treatment area with conifer removal, 2010–2017, Lake County, Oregon, USA.

Year	Annual hectares removed[a]	Cumulative hectares removed (% of total)[b]
2010	0	185 (1%)
2011	240	425 (3%)
2012	710	1,135 (8%)
2013	5113	6,248 (45%)
2014	4929	11,177 (81%)
2015	359	11,536 (83%)

Year	Annual hectares removed[a]	Cumulative hectares removed (% of total)[b]
2016	656	12,192 (88%)
2017	1,659	13,851 (100%)

[a] Includes removals within 3 km of the study area boundary.

[b] Includes area removed 2007–2009.

METHODS

Field Techniques

Field research was conducted under Oregon State University Institutional Animal Use and Care Protocol #4681. Radio collars (22 g VHF, Advanced Telemetry Systems, Isanti, Minnesota, USA) or rump-mounted GPS backpacks (22 g PTT-100 solar Argos/GPS PTT, Microwave Telemetry, Inc., Columbia, Maryland, USA; 22 g solar GPS PTT with 3.5 g Holohil PD-2 VHF transmitter attached, GeoTrak, Inc., Apex, North Carolina, USA) were fitted to female sage-grouse that we captured using a spotlighting technique (Wakkinen et al. 1992). The goal was to maintain a sample size of 40 individuals in both Treatment and Control areas prior to the start of the breeding season (defined as April–July for our study). Rump-mounted GPS backpacks were not deployed until 2015, but by 2017 all females were marked with GPS transmitters and VHF radio collars were no longer in use. Females marked with VHF transmitters were located twice per week and locations were collected from females marked with GPS transmitters 4–5 times per day during the breeding season.

Geospatial Data

All sage-grouse habitat selection predictor variables were derived from remote sensing data. A 10-m digital elevation model (DEM) was used to assign elevation to used and available locations. We calculated slope, aspect, and terrain landform, and ruggedness in buffers of radii 56, 400, and 800 m (rugged-56, landform-56, etc.) around locations using Geomorphometry and Gradient metrics Toolbox 2.0 (Evans et al. 2014). The extents encompassed the potential range of spatial scales found to be important for sage-grouse in previous studies and a 56-m buffer corresponds to approximately 1 ha (Doherty et al. 2010, Casazza et al. 2011, Baruch-Mordo et al. 2013). Ruggedness (or roughness) is a measurement of topographic heterogeneity (Riley et al. 1999) and landform is an index of landscape curvature (Bolstad and Lillesand 1992). Ruggedness values are ≥0 and larger values indicate greater topographic roughness (Riley et al. 1999). Positive values of landform indicate convex features (ridges), negative values indicate concave features (depressions), and values at or near zero indicate flat features (Bolstad and Lillesand 1992). Percent cover of conifers, shrubs, perennial forbs and grasses, and annual forbs and grasses within buffers of radii 56, 400, and 800 m (conifer-56, shrub-56, perennial-56, annual-56, etc.) around sage-grouse locations and random, available locations was derived from remotely-sensed, annual, 30-m rasters of percent cover (Jones et al. 2018; Table S1, available online in Supporting Information).

Conifer removal variables included distance to nearest conifer removal (removal-distance), years since nearest conifer removal (removal-years), and change in conifer cover. Using conifer-removal-area polygons obtained from the BLM and NRCS, the distance (m) to nearest removal polygon and years since nearest removal were assigned to used and available locations in the Treatment in ArcMap 10.2 (ArcGIS Desktop: Release 10, Environmental Systems Research Institute, Redlands, Calfironia, USA). Using 2008 as a reference, change in percent conifer cover within buffers of radii 56, 400, and 800 m (Δconifer-56, Δconifer-400, Δconifer-800) was derived from percent conifer cover metrics described above for used and available locations. Larger, negative values of Δconifer indicate greater reduction in conifer cover since 2008, positive values indicate increases in conifer cover, and values near zero indicate no change in conifer cover.

Model Development

Separate resource selection functions (RSF) of breeding season habitat selection were estimated for the Treatment and Control in the use-availability framework using mixed effects logistic regression (MELR) in the lme4 package (Bates et al. 2015) in R (R Core Team 2017). Inclusion of random effects can improve model fit and account for the spatial and temporal autocorrelation inherent to many resource selection studies using telemetry data (Gillies et al. 2006, Bolker et al. 2009). The *a priori* random effects structure for all models was a random intercept for effect of year and another for the effect of individual sage-grouse. The random effect of year was included to provide a general assessment of patterns in selection independent of annual variation in resource availability. Prior to inclusion in MELR models, the correlation of candidate covariates was assessed with Spearman rank-order correlations. Highly correlated variables ($|r| \geq 0.60$) were excluded or transformed prior to inclusion in models. Available locations for the Treatment and Control were randomly generated at a 3:1 ratio to used locations in ArcMap in minimum convex polygons of pooled, use locations from 2010–2017.

An information-theoretic approach using Akaike's Information Criterion adjusted for small sample size (AIC_c) was used to evaluate resource selection models in a 3-stage process. During stage one, we determined the most parsimonious spatial scales for variables that were measured with multiple buffers. At stage 2, we determined the most parsimonious *a priori* habitat model incorporating variables from stage one and all other non-conifer removal variables. Finally, we determined the most parsimonious *a priori* conifer removal model incorporating removal variables into the most parsimonious habitat model from stage 2 (for the Treatment only).

Marginal (only fixed effects) and conditional (fixed and random effects combined) R^2 of the most parsimonious models were calculated following Nakagawa and Schielzeth (2013) using the MuMIn package (Bartón 2014) in R (R Core Team 2017). Additionally, the variance explained by random and fixed effects from the top model was calculated using the sjstats package (Lüdecke 2018) in R (R Core Team 2017). We report coefficient estimates and 95% confidence intervals for the most parsimonious models.

Dynamics in Relative Probability of Use

Direct quantitative comparison between landscape dynamics in selection were not possible because separate RSF models were fit for the Treatment and Control and predicted probabilities of use in each area are relative to their respective available locations. Additionally, different sets of potential predictor variables were tested in the Treatment and Control because conifer removal variables were only appropriate in the Treatment RSF. For a qualitative assessment of dynamics in relative probability of use in the Treatment and Control, we plotted annual proportions of predicted values for available locations considered low (<0.25 quantile of all predicted values for a given area), medium low (≥0.25 and <0.50 quantiles), medium high (≥0.50 and <0.75 quantiles), and high (≥0.75 quantile) relative probability of use. The predicted value for a given available location (i) in the Treatment or Control (j) in a given year (k) were derived using coefficients from the most parsimonious models for Treatment and Control as follows:

$$\text{Predicted value}_{i,j,k} = e^{(\beta_1 x_{1i,j,k} + \beta_2 x_{2i,j,k} + \ldots \beta_k x_{ki})}.$$

Plots were visually inspected to assess patterns in the proportions of predicted values at the levels of relative probability of use in Treatment relative to Control.

Degree of landscape change in Treatment was assessed visually with a map of percentage change in relative probability use from 2010 to 2017. Percentage change was derived from predictive surfaces of 30-m pixels within the Treatment minimum convex polygon of sage-grouse locations across all years. Predicted values for pixels in each year were derived using the same equation as that used for predicted values at available locations described above.

RESULTS

Breeding Season Resource Selection Functions

We monitored 399 female sage-grouse during the breeding season in the Treatment ($n = 232$) and Control ($n = 167$), 2010–2017. Perennial and annual herbaceous cover were highly correlated ($r \geq 0.60$) and were combined to create a new variable, i.e., herbaceous cover (herb-56, etc.). The scale selection process for the Control indicated that landform-400, rugged-400, herb-56, and conifer-56 were the most parsimonious scales. The top habitat model for the Control indicated selection for higher elevations (β = 0.002, 95% CI = 0.002–0.002), more north facing aspects (β = 0.003, 95% CI = 0.003–0.003), greater landform-400 (ridges; β = 5.038, 95% CI = 4.493–5.582), lower rugged-400 (β = −0.028, 95% CI = −0.029–−0.027), lower herb-56 (β = −0.005, 95% CI = −0.006–0.004), greater shrub-400 (β = 0.003, 95% CI = 0.003–0.003), and lower conifer-56 (β = −13.249, 95% CI = −13.757–−12.742; Table S2, S3, available online in Supporting Information). The conditional and marginal R^2 were 0.291 and 0.278, respectively. Variance decomposition indicated that of variance explained by fixed and random effects combined, random effect of year explained 1.7%, random effect of individual explained 3.2%, and fixed effects explained 95.1%.

The most parsimonious scales for the Treatment were landform-800, rugged-56, herb-800, conifer-56, and ∆conifer-800. The top habitat model for the Treatment indicated selection for lower elevations (β = −0.004, 95% CI = −0.004–−0.003), more north facing aspects (β = 0.0006, 95% CI = 0.0003–0.0008), greater landform-800 (ridges; β = 5.464, 95% CI = 4.658–6.270), lower rugged-56 (β = −0.009, 95% CI = −0.010–−0.008), greater herb-800 (β = 0.003, 95% CI = 0.002–0.003), greater shrub-400 (β = 0.004, 95% CI = 0.002–0.005), and lower conifer-56 (β = −17.277, 95% CI = −17.904–−16.650; Table S2, S3). The conditional and marginal R^2 of the model were 0.277 and 0.265, respectively. Of the variance explained by fixed and random effects combined, fixed effects explained 95.6%, random effect of year explained 4.4%, and random effect of individual explained 0%.

The top conifer removal model indicated selection for areas in or near older conifer removal areas (β = 0.235, 95% CI = 0.218–0.251), areas closer to conifer removal areas (β = −0.00041, 95% CI = −0.00043–−0.00040), and for changes in conifer cover ±10% since 2008 (β = 0.055, 95% CI = 0.059–0.040; Table S4, S5, available online in Supporting Information; Fig. 2). The odds ratio indicated a 26.5% annual increase in probability of use of removal areas (95% CI = 24.4–28.6%). There was a decrease in probability of use of 4.1% (95% CI = 4.0–4.2%) for each 100 m distance from a removal area and a 26.5% (95% CI = 23.3–29.1%) decrease in probability of use for each 1% increase in conifer-56. Direction and significance of the effects from the habitat model were unchanged after addition of these variables (Table S4). The conditional and marginal R^2 of the model were 0.625 and 0.409, respectively. Fixed effects explained 50.0%, random effect of individual explained 1.3%, and random effect of year explained 48.7% of the variance explained by fixed and random effects combined.

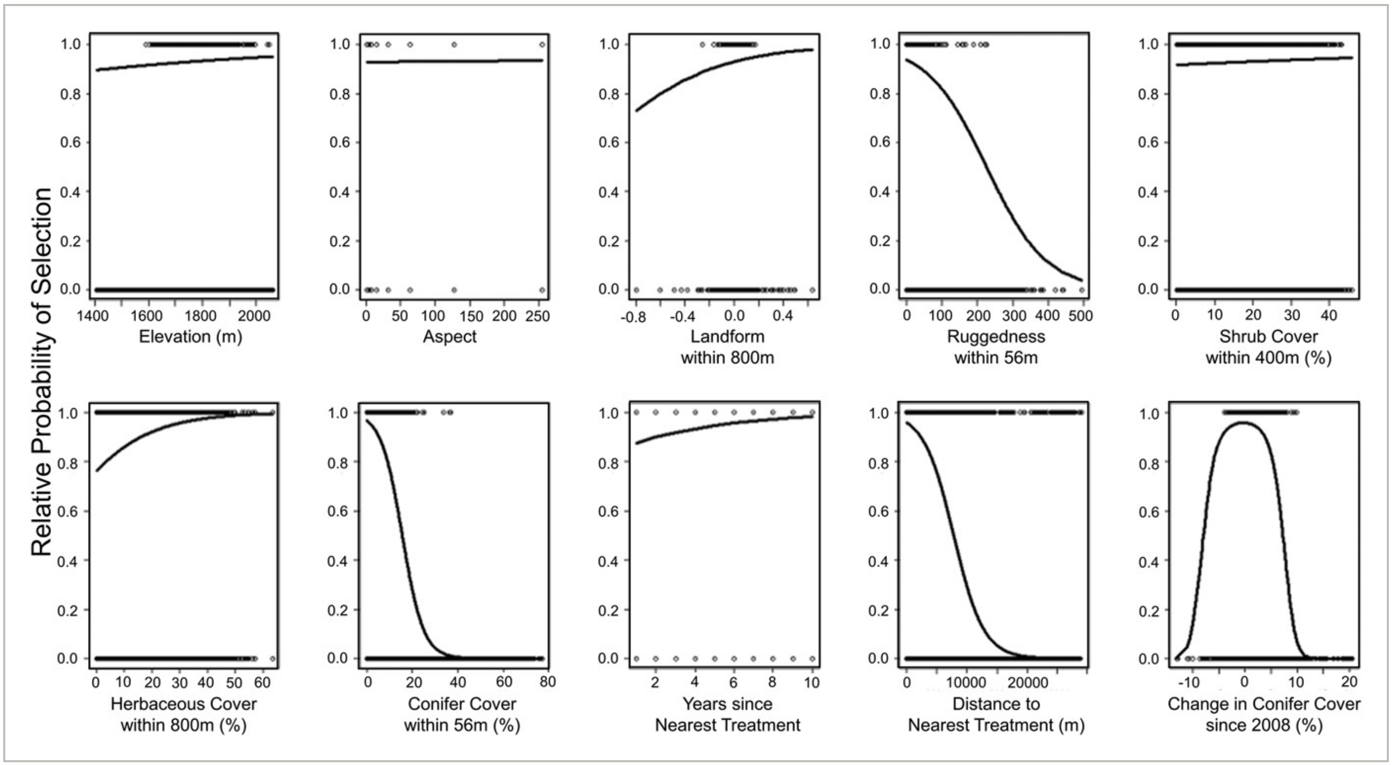

Figure 2

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Partial effects plots from a breeding season resource selection function for sage-grouse in a treatment area with conifer removal, 2010–2017, Lake County, Oregon, USA.

Dynamics in Relative Probability of Use

The proportion of available locations considered high relative probability of use in the Treatment steadily increased from 5% in 2011 to 31% in 2017; lowest relative probability of use locations decreased from 57% to 21% by 2017 (Fig. 3). Predictive surfaces indicated that approximately 81% of 30 m pixels across the Treatment experienced an increase in relative probability of use from 2010 to 2017 (Fig. 4A). This increase equates to approximately 32,000 ha of the approximately 40,000-ha study area. Relative to the Treatment, relative probability of use was stable in the Control (Fig. 4B).

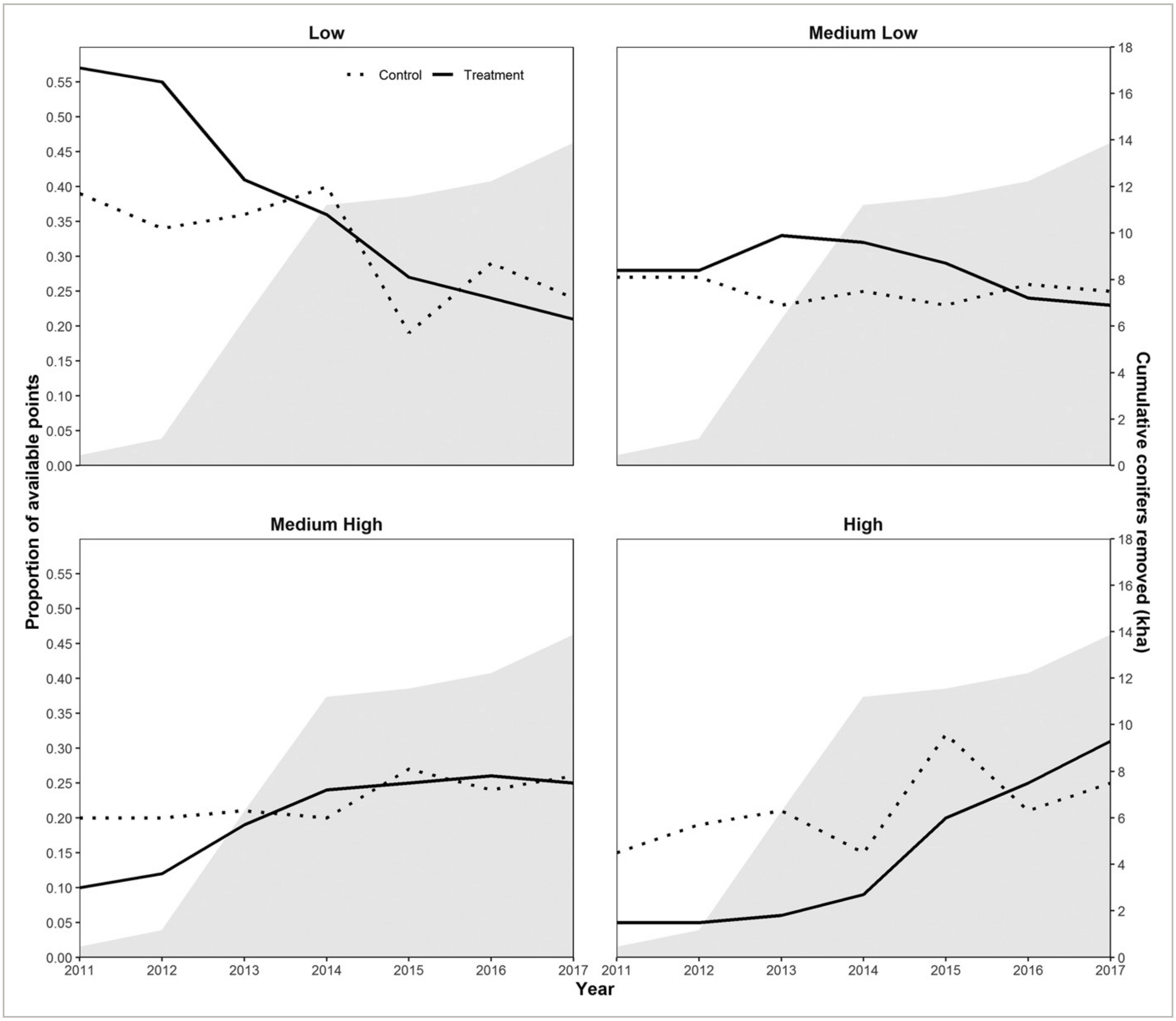

Figure 3

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Plots of proportions of predicted values for available locations considered low, medium low, medium high, and high relative probability of use based on quartiles of predicted values from breeding season resource selection functions for sage-grouse in a treatment area with conifer removal and control area without conifer removal, 2011–2017, Lake County, Oregon, USA. The shaded area represents the cumulative area of conifers removed in the treatment area.

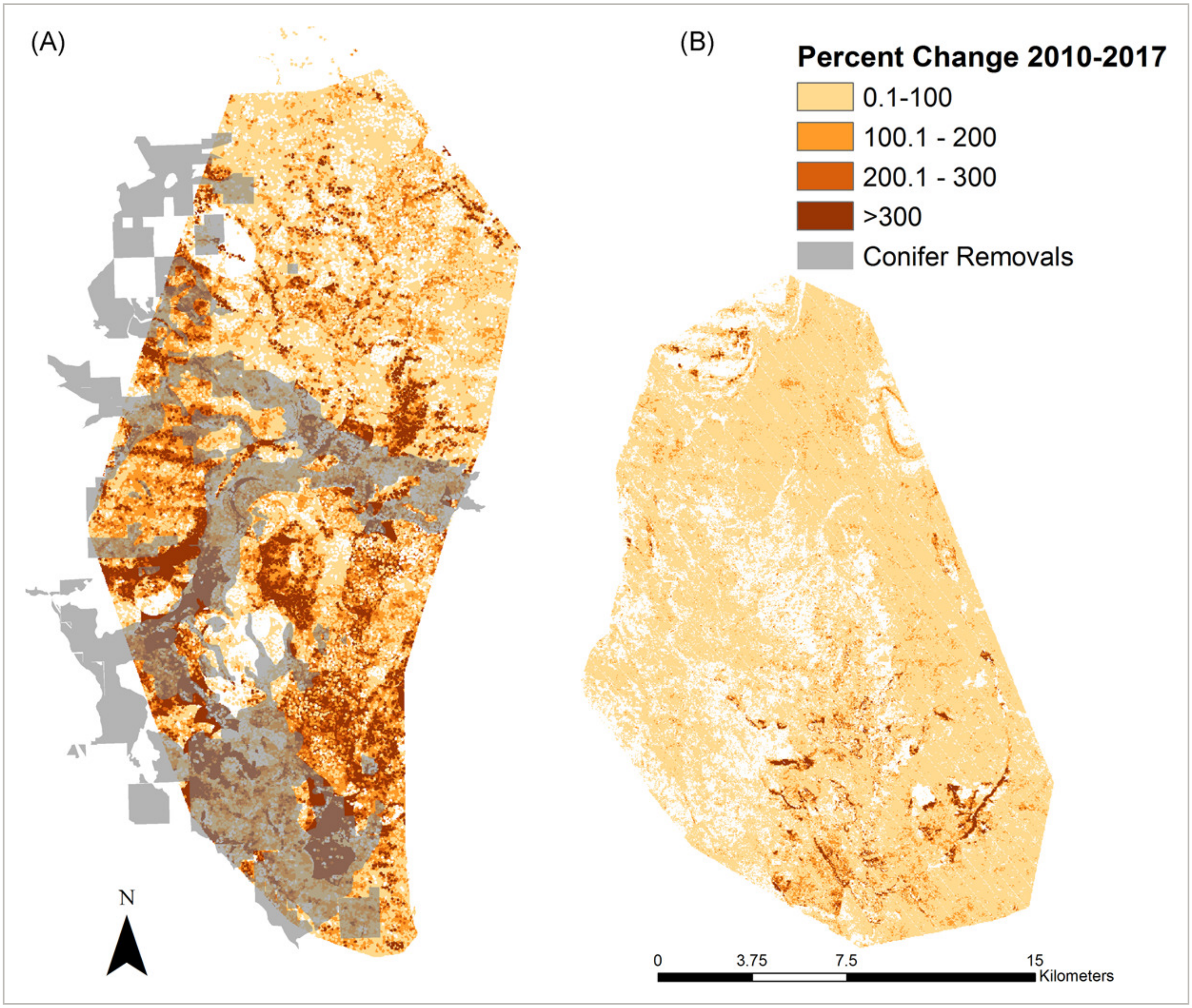

Figure 4

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Map of percentage change in sage-grouse breeding season relative probability of use in A) a treatment area with conifer removal and B) control area without conifer removal from 2010 to 2017, Lake County, Oregon, USA. Darker colors indicate greater increases in relative probability of use and gray polygons are conifer removal areas. Transparent areas indicate no increase in relative probability of use.

DISCUSSION

Conifer expansion is a widespread and serious threat to the maintenance of sagebrush ecosystems and obligate species and our findings support the hypothesis that large-scale but targeted mechanical conifer removal, such as that conducted in our study area, can be an effective method of alleviating this threat to sage-grouse. Our findings lend support to land managers that are continuing to employ these landscape restoration methods and benefit the species that inhabit ecosystems affected by conifer expansion. Current conifer removal efforts across sagebrush ecosystems in the Great Basin may not be keeping pace with the rate of conifer expansion (Reinhardt et al. 2020), and accelerated management in priority watersheds is likely needed to maintain or increase the amount of useable space for sage-grouse and other sagebrush-obligates.

Conifer cover appears to be a primary driver of sage-grouse space use in areas affected by conifer expansion as the effect of conifer cover had the largest magnitude in all of the models in our analysis (Tables S3 and S4). Our findings that sage-grouse selected breeding season habitat closer to conifer removals and were 26% more likely to use a removal each year after conifers were removed lending support to conifer removal as a tool to increase usable space and available habitat. The benefits of conifer removal for sage-grouse breeding season habitat extended beyond the bounds of the conifer removal polygons to adjacent habitat due to the distance to removal area predictor variable that indicated increasing relative probability of use in habitat closer to removals (Fig. 4A). Sage-grouse habitat management that seeks to increase available habitat in these landscapes is unlikely to be successful if it does not address conifer expansion. As conifer removals continue across the Great Basin, findings of our research provide valuable insight into the response of sage-grouse to these broad-scale management actions which historically lacked empirical evidence for their efficacy (USFWS 2015).

Given annual dynamics in herbaceous cover, the Control improved inference of conifer removal effects on available habitat in the Treatment and provided a valuable landscape-scale comparison that accounted for these precipitation-driven changes. The quadratic effect of change in conifer cover (Δconifer-800^2) had a large effect relative to other predictor variables in the top conifer removal model. Sage-grouse were highly unlikely to use habitat patches where changes in conifer cover exceeded ±10%, suggesting conifer removals that target post-European settlement conifers at ≤10% cover may have the greatest likelihood of use during the time frame examined in our study. However, given increased likelihood to select removal areas year after year, the effect on breeding season habitat selection may dampen with time and sage-grouse may use areas with greater reductions in conifer cover.

Understory response after conifer removal has been well documented and often results in rapid increase in perennial grasses and forbs after removal (Bates et al. 2005, Miller et al. 2005, Bates et al. 2017, Severson et al. 2017*c*). Herbaceous understory is an important component of sage-grouse habitat and diet, and its increase may drive the use of conifer removal areas by sage-grouse documented in our study and previous analyses (Commons et al. 1999, Frey et al. 2013, Severson et al. 2017*b*, Sandford et al. 2017). However, invasive annual grasses such as cheatgrass (*Bromus tectorum*) may also increase in conifer removal areas (Bates et al. 2005, Severson et al. 2017*c*). Localized increases in exotic annual grass cover associated with conifer removal in the project area were documented 1–3 years after removals but were not statistically significant (Severson et al. 2017*c*). Increases in annual grass cover may have been due to annual grass that was present at low levels prior to conifer removal (Davies et al. 2019). Conifer removal sites with high ecosystem resistance and resilience (Chambers et al. 2014) and adequate pre-removal perennial grass density have the greatest likelihood of native understory reestablishment post-removal (Bates et al. 2005, Davies et al. 2019).

Spatial configuration of trees has been another important determinant of sage-grouse habitat selection and the effects of conifer cover. Baruch-Mordo et al. (2013) found that leks were more likely to be active when trees were clustered as opposed to dispersed at the 5000-m scale. Severson et al. (2017*a*) examined the effect of conifer configuration on sage-grouse nest site selection. At the 800-m scale, conifer clustering index was an important predictor of sage-grouse nest site selection and indicated selection for increasingly clustered conifers and an interaction between clustering index and conifer indicated selection for areas of low conifer cover and high conifer clustering (Severson et al. 2017*a*). The conifer cover data used for their analysis consisted of individual tree locations and their associated crown diameters, which is necessary for calculation of the index (Falkowski et al. 2017, Severson et al. 2017*a*). However, the clustering index could not be derived from the 30-m rasters of conifer cover used in our analysis (Jones et al. 2018). The exclusion of conifer clustering index may limit interpretation of selection for lower conifer cover in our analyses, as the findings of Severson et al. (2017*a*) indicated differential selection within the same level of conifer cover based on clustering index. However, our analysis was the first to apply the Jones et al. (2018) annual vegetation rasters to sage-grouse habitat selection analyses and the temporal resolution of these data captured annual variability of herbaceous cover at broad scales, a variable often lacking in other sage-grouse selection studies.

Positive effects of conifer removal on habitat availability for sage-grouse may also result in demographic benefits (Sandford et al. 2017, Severson et al. 2017*d*, Olsen et al. 2021). Sage-grouse broods in Utah were more likely to be successful (≥1 chick surviving ≥50 days) when occupying habitat at lower conifer levels and closer to conifer removal areas (Sandford et al. 2017). Previous analysis in our study area indicated annual female survival increased 6.6% and nest survival increased 18.8% in the Treatment relative to the Control during the first 3 years after conifer removals were initiated (Severson et al. 2017*d*). A longer-term assessment of demographic consequences of conifer removal indicated an 11–13% increase in population growth rate (λ) in the Treatment relative to the Control 5–6 years after conifer removals began (Olsen et al. 2021). Conifer expansion may increase perch sites for avian predators of sage-grouse (Paton 1994, Wolff et al. 1999) and contribute to environments with higher risk of mortality, even when trees are sparse and scattered (Coates et al. 2017, Prochazka et al. 2017).

Sage-grouse perception of this risk may be the mechanism behind avoidance of conifers in our study and others (Baruch-Mordo et al. 2013, Coates et al. 2017, Severson et al. 2017*a*).

MANAGEMENT IMPLICATIONS

Managers should target conifers at ≤10% cover with intact sagebrush and bunchgrass understory for the greatest increases in sage-grouse use over the time frame examined in our study (1–5 years after removals initiated) and in comparable landscapes in the northern Great Basin. However, sage-grouse are increasingly likely to use areas where conifers are removed, and removal projects adjacent to occupied sage-grouse habitat that target conifers with >10% cover and retain or restore sagebrush and bunchgrass understory will likely benefit sage-grouse long-term. Whereas the effects of conifer expansion on sage-grouse habitat selection are scale dependent, large-scale, contiguous removals in priority watersheds are likely to maintain or create the most usable space for sage-grouse.

ACKNOWLEDGMENTS

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Supporting Information

Additional supporting material may be found in the online version of this article at the publisher's web-site. This material includes RSF model coefficients and summary statistics for vegetation data.

Filename	Description
wsb1214-sup-0001-Olsenetal_SupMat.pdf 62.9 KB	Supporting Information

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