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Research Article

Effects of Conifer Expansion on Greater Sage-Grouse Nesting Habitat Selection

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ABSTRACT Expansion of conifer woodlands into sagebrush (*Artemisia* spp.) ecosystems is a primary threat to the greater sage-grouse (*Centrocercus urophasianus*) in the Great Basin, southeast Oregon, USA. Conifer removal to restore sage-grouse habitats has been widely implemented, yet limited information exists on the effects of conifer expansion on sage-grouse habitat selection. Our objective was to evaluate the landscape-scale effects of conifer expansion on selection of sites for nesting and to estimate direction, magnitude, and scale of effects. We classified 160 nests and 167 available sites with random forests during 2010–2011 to assess effects of conifer cover and tree clustering at multiple scales along with other vegetation and topographic covariates on selection of nesting habitat. Relative probability of nesting was negatively associated with >3% conifer cover within 800 m of nests. When trees were present within 800 m of nests, sage-grouse nested where trees were clustered rather than dispersed, suggesting selection for more open habitat. Results further indicated that sage-grouse are nesting in landscapes susceptible to conifer expansion that have yet to be invaded. Sage-grouse are expected to lose nesting habitat as conifer expansion continues, but management intervention may be a possible solution to increase habitat availability where open space for nesting is a limiting factor. © 2016 The Wildlife Society.

KEY WORDS *Centrocercus urophasianus*, conifer expansion, Great Basin, *Juniperus occidentalis*, sagebrush, sage-grouse, western juniper.

Greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) require large, contiguous tracts of sagebrush (*Artemisia* spp.)-dominated shrub-steppe in western North America (Knick and Connelly 2011, U.S. Fish and Wildlife Service [USFWS] 2015). Sage-grouse distribution has declined by half since European settlement (Schroeder et al. 2004) with myriad threats contributing to habitat loss, fragmentation, and continued degradation. Top-down threats identified by USFWS (2015) include catastrophic wildfire (Miller et al. 2011, Murphy et al. 2013), invasive annual grasses (Davies et al. 2011), energy development (Walker et al. 2007, Holloran et al. 2010, Taylor et al. 2013), and conversion of sagebrush ecosystems to cropland (Smith et al. 2016). Consequently, sage-grouse have been considered multiple times for protection under the federal Endangered Species Act (ESA; Stiver 2011, USFWS 2015), most recently prompting an unprecedented range-wide conservation response to reverse long-term trends and obviate the need for additional regulation (USFWS 2015).

Expansion of coniferous trees into sagebrush ecosystems is one primary threat of increasing conservation interest (Baruch-Mordo et al. 2013). Native piñon (*Pinus* spp.) and juniper (*Juniperus* spp.) woodlands have expanded by 625% (Miller and Tausch 2001, Miller et al. 2008) largely at the expense of sagebrush ecosystems (Miller et al. 2011). For example, western juniper (*J. occidentalis*), the most abundant conifer in the northern Great Basin shrub-steppe, has increased 10-fold in the past 130 years in the Intermountain West and currently occupies 3.6 million ha in California, Nevada, Idaho, Oregon, and Washington (Miller and Tausch 2001, Miller et al. 2005). The inverse relationship between sagebrush and conifer cover (Miller et al. 2011) has implications for sage-grouse and other species dependent upon sagebrush habitats. As woodland succession progresses, shrub and herbaceous vegetation abundance and diversity decreases because of competition for limited resources, resulting in accelerated surface water runoff and topsoil erosion (Buckhouse and Gaither 1982, Gaither and Buckhouse 1983, Miller et al. 2005). Soil water availability is also reduced in conifer-dominated landscapes (Roundy

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et al. 2014, Kormos et al. 2017), which may affect mesic riparian and meadow areas necessary for sage-grouse brood-rearing (Atamian et al. 2010, Donnelly et al. 2016). Although some woodland guilds (e.g., tree and cavity nesters) of birds may benefit from conifer expansion, grassland and sagebrush obligates of high conservation concern decline with increasing conifer (Coppedge et al. 2001, Rosenstock and Van Riper 2001, Reinkensmeyer et al. 2007).

Several studies considering conifer cover as a covariate in sage-grouse models have indicated avoidance or negative demographic consequences of conifer expansion. Knick et al. (2013) reported most active leks average <1% conifer forest within 5 km using 90-m land cover data. Sage-grouse did not nest in juniper habitat in southeast Oregon (Gregg 1991) and they avoided nesting within 100 m of conifers in Montana (Doherty et al. 2010). In Nevada, sage-grouse broods avoided piñon-juniper and had decreased survival in areas with higher piñon-juniper coverage (Atamian et al. 2010, Casazza et al. 2011). Sage-grouse also avoided conifers during winter in Montana and Oregon (Doherty et al. 2008, Freese 2009). Furthermore, increasing conifer abundance was associated with decreased lek occupancy in Oregon (Baruch-Mordo et al. 2013). Tree expansion can increase perch availability for avian predators (Paton 1994, Wolff et al. 1999, Manzer and Hannon 2005), which may create an ecological trap resulting in lower sage-grouse survival (Coates et al. 2017, Prochazka et al. 2017). Although these studies indicate potential negative relationships between conifer and sage-grouse, no studies have directly assessed effects of conifer expansion on sage-grouse selection of sites for nesting using high resolution conifer data.

We evaluated the influence of conifer cover and its spatial configuration at multiple scales on sage-grouse selection of sites for nesting using high resolution (i.e., 1 m) conifer data in southeast Oregon, USA. Because sage-grouse require open spaces and previous research has shown avoidance of trees, we predicted that sage-grouse would nest in areas with less conifer cover. Additionally, because spatial configuration may change the birds' perception of available open habitat, we predicted that clustering of trees would increase the probability of nesting (Baruch-Mordo et al. 2013). We estimated cover and configuration of conifer at multiple scales around nests and predicted greater effects at broader extents because of the landscape-scale requirements of sage-grouse. Our research sought to understand impacts of conifer expansion on sage-grouse, and to inform future conifer management strategies.

STUDY AREA

Our study area was located in Oregon where western juniper expansion is considered a top-down threat constraining sage-grouse populations at mid- to high-elevation (e.g., 1,600–2,200 m; Hagen 2011). We collected data in an area 20 km by 100 km in Lake County, south-central Oregon, between the Warner Mountains and the Warner Valley extending into Modoc County, California and into Washoe County, Nevada (Fig. 1). Elevation ranged from 1,360 m to 2,180 m with an average of 1,700 m above sea level. Average annual temperature from 2000 to 2015 was 8.9°C (range: 6.4–11.8°C) and was 9.0°C in 2010 and 8.1°C in 2011. Average annual precipitation from 2000 to 2015 was 17.7 cm (range: 11.0–32.9 cm) and was 19.7 cm in 2010 and 14.6 cm in 2011. On average, the warmest and driest months were July (21.9°C; 0.5 cm precipitation) and August (21.2°C; 0.1 cm precipitation). The coolest months were January (0.6°C) and December (−0.1°C), and the wettest months were April (2.2 cm precipitation), May (2.4 cm), and December (3.1 cm precipitation).

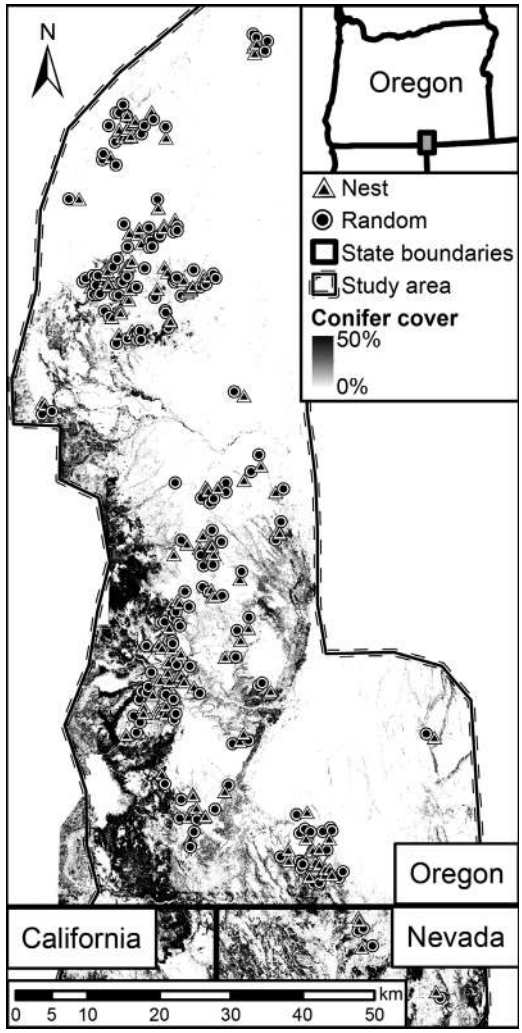

Figure 1. Study area in southeast Oregon, USA, with the Warner Mountains on the left and Warner Valley on the right and nests of greater sage-grouse, 2010–2011, depicted as stars. The base map depicts the conifer cover. Inset shows study area location in Oregon.

Dominant fauna included pronghorn (*Antilocapra americana*), coyotes (*Canis latrans*), greater sage-grouse, ravens (*Corvus corax*), and various raptor species (Accipitridae). Dominant plant species was low sagebrush (*Artemisia arbuscula*), but other important species included mountain big sagebrush (*A. tridentata vaseyana*) at higher elevations (~>1,700 m), Wyoming big sagebrush (*A. t. wyomingensis*) at lower elevations (~<1,500 m), and other interspersed shrub species including antelope bitterbrush (*Purshia*

tridentata), rabbitbrush (*Chrysothamnus* spp. and *Ericameria* spp.), saltbrush (*Atriplex* spp.), snowberry (*Symphoricarpos* spp.), and mountain mahogany (*Cercocarpus* spp.). Western juniper occurred in a patchy distribution from mid to high elevation ($\bar{x}$: 1,810 m; 95% distribution: 1,460–2,160 m).

METHODS

Nest and Available Locations

We captured female sage-grouse in winter and spring 2009–2011 using spotlighting techniques (Giesen et al. 1982, Wakkinen et al. 1992) near leks and within wintering habitats and fitted them with radio collars (22-g very high frequency radio-collars; Advanced Telemetry Systems, Isanti, MN). Capture and handling methods were approved by the Oregon Department of Fish and Wildlife (Permit No. 008-12). We monitored marked sage-grouse using radio-telemetry 2 times/week during the potential nesting seasons 2010 and 2011 until they began to occupy nesting habitat and were observed in the same place on consecutive locations. We then visually observed nesting females without flushing, and monitored nests twice weekly until incubation was terminated (e.g., hatched, depredated).

When all nest locations were known each year, we produced fixed kernel probability distributions using the median nearest neighbor distance between nests as the bandwidth with the package adehabitatHR (Calenge 2006) in the R 3.2.2 computing environment (R Core Team 2015). To estimate available nesting habitat, we populated a number of random points equal to the number of nests in the area between the 75% and 95% kernel density contours (modified from Hagen et al. 2005) while restricting the points to greater than the minimum nearest neighbor distance of nests using ArcGIS 10.0 (Environmental Systems Research Institute, Redlands, CA). We used this method as an approximation to unused or minimally used habitat by sampling in available (i.e., within the 95% utilization distribution) but low probability habitat (i.e., outside the 75% utilization distribution). We used site-scale vegetation variables measured in the field at nests and available sites and landscape variables measured from remotely sensed data (Brennan et al. 2002, Stiver et al. 2015).

Field-Collected Data

We surveyed vegetation at nests and available points in late May to early July each year after nest termination. We positioned an array of 2 10-m orthogonal transects in a random orientation centered on the nest bowl or available point. We used the line intercept method (Canfield 1941) to estimate percent cover for each shrub species and divided shrub cover into <40 cm and >40 cm tall (Connelly et al. 2000). We omitted overstory juniper cover (>2 m) from shrub cover estimates because it was not part of the shrub community and therefore not likely to influence sage-grouse decisions on nesting cover; we included short junipers (<2 m) in shrub cover estimates. We removed data within 1 m of the center of crossed transects from the shrub cover estimate to reduce bias induced from centering on the nest shrub (Musil 2011). We summarized data into total shrub cover, total sagebrush cover, shrub cover >40 cm tall, and sagebrush cover >40 cm tall because sagebrush stands >40 cm may be more productive nesting habitat (Connelly et al. 2000). We also classified the vegetation by dominant shrub type as Wyoming big sagebrush, Wyoming big sagebrush/low sagebrush association, low sagebrush, low sagebrush/bitterbrush association, mountain big sagebrush, or mountain shrub, which was generally dominated by mountain big sagebrush with a diverse association of other shrubs (e.g., bitterbrush, mahogany, and snowberry; Gregg 1991).

We measured grasses and forbs using 10 20×50-cm frames placed at intervals of 1, 3, 5, 7, and 9 m along each transect (Daubenmire 1959). In each frame, we estimated total forb cover and total key forb cover consisting of 16 taxa important to nesting and brood-rearing grouse (Barnett and Crawford 1994, Drut et al. 1994, Gregg 2006). Key forbs included desert parsley (*Lomatium* spp.), hawksbeard (*Crepis* spp.), false dandelion (*Agoseris* spp.), milkvetch (*Astragalus* spp.), broomrape (*Orobanche* spp.), clover (*Trifolium* spp.), slender phlox (*Phlox gracilis*), fleabane daisy (*Erigeron* spp.), common dandelion (*Taraxacum officinale*), goatsbeard (*Tragopogon dubius*), yarrow (*Achillea millefolium*), aster (*Aster* spp.), monkeyflower (*Mimulus* spp.), groundsmoke (*Gayophytum* spp.), pussytoes (*Antennaria* spp.), and eye-lashweed (*Blepharipappus* spp.). We also estimated total grass cover, total herbaceous cover, and herbaceous cover >18 cm tall (Connelly et al. 2000). Herbaceous variables in the analysis included key forb richness, key forb cover, total forb cover, total grass cover, total herbaceous cover, and tall herbaceous cover.

Geospatial Data

We acquired remotely sensed, 1-m resolution tree canopy data from the Natural Resources Conservation Service (Falkowski et al. 2017). Data included location and estimated crown diameter of individual conifer trees as mapped by spatial wavelet analysis (Falkowski et al. 2006, 2008; Strand et al. 2006). We quantified percent conifer canopy cover around nests and available locations in a geographic information system (GIS) to evaluate habitat selection at 6 scales: 50-, 100-, 200-, 400-, 800-, and 1,200-m-radius buffers. We selected the 2 largest extents to capture landscape processes thought to influence habitat selection (e.g., topography [Doherty et al. 2010], conifer expansion [Baruch-Mordo et al. 2013]). We also matched the largest extent sampled to our data; 1,200 m was the shortest maximum distance from the sampling points to the edge of the conifer layer. We selected 3 intermediate scales (i.e., 100, 200, 400 m) as potential surrogates for mechanisms such as predation and habitat heterogeneity that influence selection at these scales (Aldridge and Boyce 2007). We chose the 50-m scale to ensure that any local-scale relationships did not exceed the resolution of the conifer layer. We calculated a clustering index at each scale by dividing the average nearest neighbor distance among trees by the expected distance with random dispersion. An index of 1 was random, <1 was increasingly clustered, and >1 was increasingly dispersed.

Terrain can affect sage-grouse habitat use; nesting females prefer flat to rolling topography (Yost et al. 2008, Doherty et al. 2010, Aldridge et al. 2012, Baruch-Mordo et al. 2013).

We included topographic metrics to reduce unexplained model variation. We used a 10-m resolution digital elevation model (DEM; U.S. Department of Agriculture, Geospatial Data Gateway, https://gdg.sc.egov.usda.gov/, accessed 15 Jul 2013) to assign elevation, slope, and aspect values to each nest and available point. Additionally, we calculated terrain ruggedness and landform (i.e., terrain curvature) at 100-, 400-, and 1,200-m scales using the Geomorphometry and Gradient Metrics Toolbox (version 2.0, http://evansmurphy.wix.com/evansspatial, accessed 2 Dec 2014) in ArcGIS. Ruggedness represents variability in elevation (Riley et al. 1999), and landform represents concavity (i.e., depression) or convexity (i.e., ridge; McNab 1989, Bolstad and Lillesand 1992). Ruggedness index units are arbitrary, but 0 indicates flat terrain and increasing values indicate more rugged terrain. Landform units also are arbitrary, but 0 is flat, <0 is a depression, and >0 is a ridge. We also calculated distance from nests to active leks to evaluate whether proximity played a role in habitat selection.

Data Analysis

We used the random forest classification approach (Breiman 2001) to discriminate between nests and available sites. Random forest is a flexible, nonparametric classification method that builds an ensemble of thousands of classification trees developed from random features and improves upon the predictive accuracy of an individual tree (Hastie et al. 2009). For each tree, a bootstrap sample is drawn from the data to use as the training set (i.e., bag sample), and because samples are drawn with replacement, approximately 36% of samples are held out to test the finished tree (i.e., out-of-bag [OOB] sample; Breiman 2001). At each node (i.e., split) of the tree, a random subset of variables equal to $\sqrt{p}$ is drawn, where p is the total number of predictor variables, and the predictor in the subset that produces the greatest separation between the categories (e.g., nest or available) is selected for that node. The tree is grown out to maximum depth where every bagged sample is classified correctly and is then tested with the OOB sample (Breiman 2001). Random forest uses all trees to predict new data and estimate the overall OOB error rate. Random forest classifiers are resistant to collinearity of covariates, do not assume independence of samples, can model non-linear relationships, inherently consider interactions among covariates, and often perform better (i.e., lower error rates) on ecological data than parametric models such as logistic regression (Breiman 2001, Cutler et al. 2007, Evans et al. 2011). However, multidimensional collinearity can affect interpretation of results (Murphy et al. 2010). Also, although all predictors can be retained in the final model, variable reduction may decrease error and improve interpretation and variable selection methods have been suggested (Liaw and Wiener 2002, Ishwaran et al. 2010, Murphy et al. 2010, Evans et al. 2011).

We conducted a multi-stage analysis similar to Baruch-Mordo et al. (2013) where we removed multi-collinear variables, selected appropriate scales for conifer characteristics, and conducted a final model selection. We assessed multi-collinearity in the predictors using qr matrix decomposition (threshold = 0.05; Murphy et al. 2010) using the multi.collinear function in the rfUtilities package (version 1.0-0, http://cran.r-project.org/package=rfUtilities, accessed 15 Dec 2015) in the R. We applied a random forest by producing 5,000 classification trees with function randomForest in the randomForest package (version 1.6.0, https://cran.r-project.org/web/packages/randomForest/, accessed 20 Feb 2015) to these variables with nest versus available as the response. We determined bagged samples by bootstrapping, assessed $\sqrt{p}$ variables at each node, and grew trees to maximal depth. The OOB error can be slightly biased and variable; one way to produce more stable and precise estimates of error is cross-validation (Liaw and Weiner 2002, Evans et al. 2011). To determine optimal scale of selection, for each pair of conifer characteristics (i.e., clustering and canopy cover) at each scale, we calculated the mean test error from 30 iterations of 10-fold cross-validation using the errorest function in the ipred package (version 0.9-3, https://cran.r-project.org/web/packages/ipred, accessed 20 Feb 2015). The cumulative standard errors of the cross-validation error rates generally were variable up to approximately 10–15 iterations, followed by a systematic decrease and were below 0.5 percentage points for all models by <25 iterations, which we deemed an acceptable precision. To further test importance of conifer, we conducted cross-validation analysis for the best scale of clustering and of canopy cover, each in turn, and then evaluated a model absent conifer variables.

Using the model with the lowest cross-validation error rate from the previous analysis, we then conducted variable selection with the rf.modelSel function in the rfUtilities package to iterate through various thresholds (0–1, by 0.1 increments) of model improvement ratios of each variable and selected the model that minimized OOB error (Murphy et al. 2010). We calculated accuracy of the final model with OOB error rate, cross-validation error rate, and class error rates to ensure balance in nest-site and available-site classification.

We then calculated the relative importance and produced partial dependence plots of the marginal selection response for each predictor in the final model. We also constructed an interaction plot for conifer clustering and conifer cover by holding all other covariates at their median and predicting an array of clustering and cover values. For selected factor variables (e.g., shrub type), we calculated the 95% confidence intervals from 500 bootstraps of the random forest model to complement point estimates of relative nesting probability for each category.

RESULTS

We located and surveyed 160 nests and 167 available points in 2010 and 2011 (Fig. 1). Total herbaceous cover and conifer canopy cover at 50-, 100-, and 200-m scales were multi-collinear. We removed herbaceous cover, but because we were interested in conifer at multiple scales, we proceeded to test all scales of conifer characteristics with the caveat that interpretation may be degraded if these smaller extents were selected. The 800-m scale had the smallest cross-validation error (29.1%) followed by 1,200 m (30.0%), 400 m (33.1%),

50 m (34.7%), 200 m (35.1%), and 100 m (35.6%). Without any conifer characteristics, the model had a 32.9% cross-validation error rate. At the 800-m scale, when we removed conifer canopy cover and conifer clustering in turn, cross-validation error increased in both cases (canopy cover: 30.7%; clustering: 30.0%) indicating that both variables warranted inclusion.

Because the conifer clustering index was undefined with no trees present, only sites with conifers within 800 m could be used in the analysis, resulting in a sample size of 153 nests and 152 available sites. When we applied the model selection function to the model with the 800-m scale conifer characteristics, 12 of 23 variables remained (Fig. 2) with an OOB error of 26.9% and a cross-validation error of 27.4%. Nest-site OOB error was 30.0%, whereas the available-site OOB error was 23.4%. The random forest error stabilized at approximately 2,000 trees, indicating that 5,000 trees was adequate.

Our best model included relationships with both conifer metrics, along with 10 additional habitat features that varied predictably in direction and magnitude given what is reported in the sage-grouse nesting literature (Fig. 2). Shrub cover was the most important variable explaining the selection of a site for nesting followed by forb cover (Fig. 2).

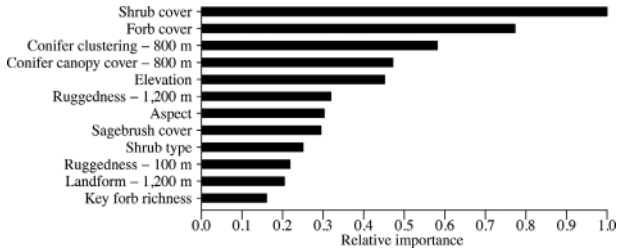

Figure 2. Relative importance (standardized to 1) of variables from a random forest model of greater sage-grouse selection of sites for nesting in southeast Oregon, USA, 2010–2011. The number in the variable represents the selected scale (radius in m) around the nest or available site; shrub and forb cover were measured within 5 m of the site, and elevation, aspect, and slope were measured from the 10-m resolution digital elevation model.

Conifer clustering and conifer cover were the next most important followed by the other variables (Fig. 2).

Probability of selecting a site for nesting increased gradually with increasing shrub cover to 55% cover and then began to decline (Fig. 3A). Response to sagebrush cover increased sharply up to 10%, then subsequently peaked at 50% (Fig. 3B). Response to forb cover increased to 2–3% cover, then leveled off (Fig. 3C). Key forb richness increased to 2 species and then increased gradually (Fig. 3D). Nesting

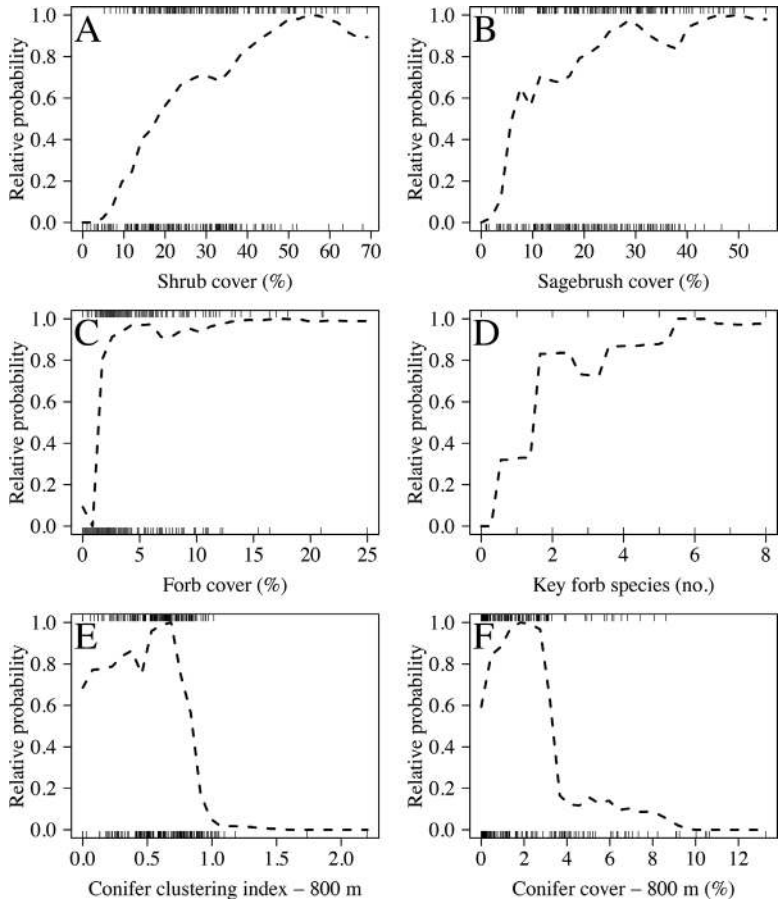

Figure 3. Partial dependence plots for vegetation and conifer characteristics with relative probability of greater sage-grouse selection of sites for nesting in southeast Oregon, USA, 2010–2011. Tick marks at the top of the plots are data at nests and tick marks at the bottom are data at available sites. Shrub cover (A), sagebrush cover (B), forb cover (C), and key forb richness (D) were measured within 5 m of the sites. Conifer clustering index (E) and conifer canopy cover (F) were measured within 800 m.

grouse selected more clustered instead of dispersed conifer trees at an intermediate scale (800-m) scale (Fig. 3E). At the same scale, nesting was improbable with conifer cover >3% (Fig. 3F). The interaction between conifer cover and clustering revealed increased nesting in low cover areas with clustered trees and avoidance of high cover areas with dispersed trees (Fig. 4).

There was a low probability of selecting low elevations for nesting, but the probability increased to a peak at mid elevation (1,656 m) and remained moderately high at high elevations (Fig. 5A). Nesting sage-grouse selected north, northeast, east, and southeast slopes (Fig. 5B), less rugged terrain near nests (100 m; Fig. 5C), and moderately rugged terrain at a broader extent (1,200 m; Fig. 5D). They also selected ridges (1,200 m; Fig. 5E) and mountain shrub habitats, followed by other vegetation types (Fig. 5F).

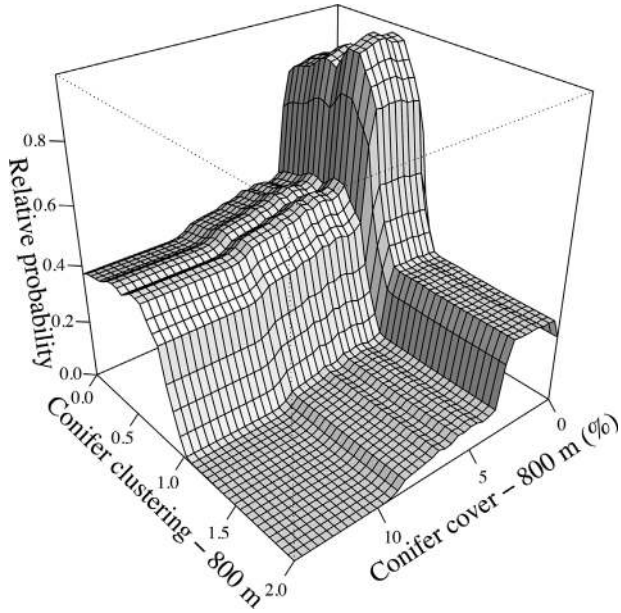

Figure 4. Partial dependence plot of relative probability of greater sage-grouse selection of sites for nesting and a conifer cover and conifer clustering interaction in southeast Oregon, USA, 2010–2011.

DISCUSSION

Our study is one of the first empirical studies quantifying the negative effects of conifer expansion on sage-grouse selection of nesting habitat and is the first to document the role of spatial configuration of trees on nesting. Nesting females avoided conifer within a 2-km^2 area (800-m radius) around

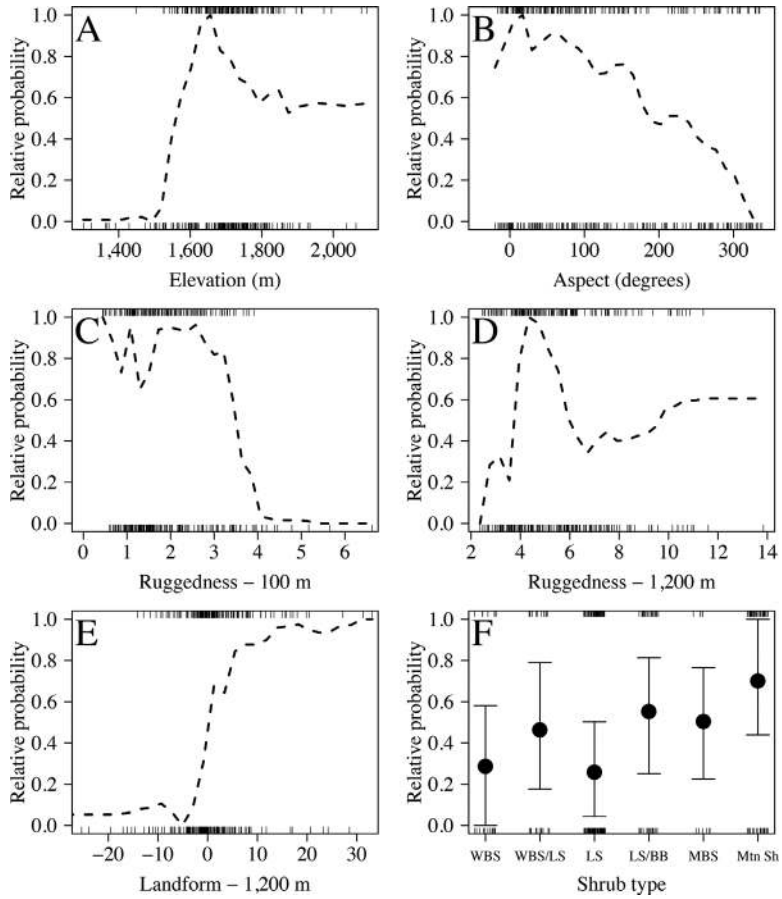

Figure 5. Partial dependence plots for terrain characteristics and shrub type with relative probability of greater sage-grouse selection of sites for nesting in southeast Oregon, USA, 2010–2011. Tick marks at the top of the plots are data at nests and tick marks at the bottom are data at available sites. Elevation (A) and aspect (B) were measured within a 10-m resolution pixel in the digital elevation model. Ruggedness was measured within 100 m (C) and 1,200 m (D) of the sites and landform was measured within 1,200 m (E) of the sites. Shrub type (F) was classified within 5 m of the sites. Error bars represent bootstrapped 95% confidence intervals. WBS: Wyoming big sagebrush; LS: low sagebrush; BB: bitterbrush; MBS: mountain big sagebrush; Mtn Sh: mountain shrub.

nests when seemingly benign levels of conifer cover (i.e., 3%) were present on the landscape (Fig. 3F). Previous research in Oregon demonstrated similarly low thresholds for conifer in breeding (4%; Baruch-Mordo et al. 2013) and wintering areas (5%; Freese 2009). When conifers were present, sage-grouse nested in areas where trees were more clustered than dispersed, which we attributed to increased availability of open, treeless interspaces in areas with clumped trees. Likewise, Baruch-Mordo et al. (2013) observed decreasing lek occupancy as trees become more dispersed rather than clustered suggesting that female sage-grouse eventually abandon habitats when trees become too pervasive across the landscape.

Shrub cover was the most important variable in selecting sites for nesting (Fig. 2), which was consistent with the results of a meta-analysis showing the relative importance of total shrub cover (Hagen et al. 2007). Selection for areas with low levels of conifer cover, but acceptable shrub cover, is concerning and generates questions about sage-grouse habitat selection decisions. Although shrub cover declines with increasing conifer cover (Miller et al. 2011), it is unlikely that low amounts of conifer (i.e., <3% cover) in the early phases of woodland succession would produce measurable decreases in shrub cover (Miller et al. 2005). Sage-grouse may perceive these areas with less tree cover as suitable habitat where demographic benefits of increased shrub cover or the associated productive habitat override risks associated with short conifer trees or less conifer abundance. However, research is needed to determine whether these areas are functioning as an ecological trap (Coates et al. 2017, Prochazka et al. 2017) due to increased avian predator perches and nesting sites that may result in increased predation risk to sage-grouse and their nests. Further, the observation that otherwise suitable nesting areas were rendered unsuitable with little conifer cover on the landscape is alarming given the large spatial extent of conifer expansion (Miller and Tausch 2001, Miller et al. 2008). Amount of nesting habitat would be expected to decrease through time because the types of sagebrush communities most readily selected by nesting females in this study (i.e., low sagebrush/bitterbrush, mountain big sagebrush, and mountain shrub) are also those most susceptible to continued conifer expansion and infill (Miller and Eddleman 2001, Davies et al. 2011).

Sage-grouse in our study area nested in landscapes characterized by flat to rolling terrain on mid- to high-elevation ridges, and either in or near mountain big sagebrush or mountain shrub habitat with increased shrub and forb abundance. Researchers in Oregon, Montana, and Colorado have reported effects of topographic features on sage-grouse habitat selection (Yost et al. 2008, Doherty et al. 2010, Aldridge et al. 2012, Baruch-Mordo et al. 2013), but we found site-scale and landscape-scale vegetation characteristics to be relatively more influential than terrain in selecting nesting habitat. Regardless, this combination of terrain and vegetation indicate female selection for nesting in areas with greater moisture and nutrient availability (McNab 1993). Unfortunately, the vulnerability of these community types to conifer expansion (Miller and Eddleman 2001, Miller et al. 2005) may present a tradeoff in selection between high productivity habitats with trees and low productivity landscapes without them.

Conifer management may be beneficial in restoring and maintaining sage-grouse habitat where conifer expansion is limiting habitat availability, but there is paucity of research on the effects of conifer removal to sage-grouse (USFWS 2015). Although lacking adequate study designs to conclusively attribute observed responses to conifer removal, previous research has indicated possible benefits, including increased population size and habitat availability, as a result of removing conifer in sage-grouse habitat (Commons et al. 1999, Frey et al. 2013). Sage-grouse in our study area have shown potential increases in nest survival and female survival at a landscape scale and increased use of nesting and seasonal habitat following conifer removal (Severson 2016, Severson et al. 2017). However, more experimental studies assessing both changing space use and population demographics are needed to verify the efficacy of conifer removal for sage-grouse management.

We encourage some caution with interpretation of exact threshold values from our work because conifer covariates were derived from modeled surfaces in a GIS. Data used were produced from spatial wavelet analyses on the normalized difference vegetation index of 4-band, 1-m resolution aerial imagery (Falkowski et al. 2006, Strand et al. 2006). Ground-based estimates of cover using traditional methods, such as line intercept, would likely yield slightly different cover estimates than remote sensing data (Ko et al. 2009). Poznanovic et al. (2014) reported high correlation between the wavelet data and reference plots, but wavelet data slightly underestimated canopy cover because younger, shorter trees still below the height of sagebrush may not be detected (Strand et al. 2006). However, larger trees may have more impact on the habitat and sage-grouse behavior than smaller trees (Baruch-Mordo et al. 2013) because small trees blend in with the rest of the shrub community and, at this growth stage, perches and nest sites for avian predators remain limited. These remotely sensed data are increasingly being used by land managers and researchers as they become available, thereby allowing our results to be comparable to their assessments.

MANAGEMENT IMPLICATIONS

Our results further confirm the negative effects of conifer expansion on sage-grouse habitat and suggest, at a minimum, that nesting habitat availability will become increasingly limited as woodland expansion and infill continues. Limiting conifer expansion may be necessary to maintain current nesting habitat. To maintain nesting habitat, our results suggest management intervention may be needed to reduce conifer to <3% canopy cover over at least a 200-ha area (i.e., 800-m radius around potential nest sites); if any trees remain below this threshold, our results also suggest they should be clustered and in more rugged terrain to minimize impacts on nesting habitat potential. However, conifer removal can also increase available nesting habitat (Severson et al. 2017). The strong selection for increased shrub cover that we observed suggests that if conifers are removed to increase nesting habitat for sage-grouse, the removal technique should

minimize impact to shrubs. For example, hand cutting may be more beneficial than removal with heavy machinery or broadcast burning that can result in shrub cover reduction. Also, removing conifers in and adjacent to large, intact shrubland may expand nesting habitat more quickly than isolated patched cuts deep in conifer woodland. Our findings, combined with growing experimental evidence of space use and fitness consequences of conifer expansion and removal (Severson 2016, Coates et al. 2017, Prochazka et al. 2017, Severson et al. 2017), lend support to the inclusion of conifer removal as a proactive strategy for addressing a key threat to sage-grouse habitat (Baruch-Mordo et al. 2013, USFWS 2015).

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