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Saving sage-grouse from the trees: A proactive solution to reducing a key threat to a candidate species

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ABSTRACT

Conservation investment in management of at-risk species can be less costly than a delay-and-repair approach implemented after species receive legal protection. The United States Endangered Species Act candidate species designation represents an opportunity to implement proactive management to avoid future listing. Such efforts require substantial investments, and the challenge becomes one of optimization of limited conservation funds to maximize return. Focusing on conifer encroachment threats to greater sage-grouse (*Centrocercus urophasianus*), we demonstrated an approach that links species demographics with attributes of conservation threats to inform targeting of investments. We mapped conifer stand characteristics using spatial wavelet analysis, and modeled lek activity as a function of conifer-related and additional lek site covariates using random forests. We applied modeling results to identify leks of high management potential and to estimate management costs. Results suggest sage-grouse incur population-level impacts at very low levels of encroachment, and leks were less likely to be active where smaller trees were dispersed. We estimated costs of prevention (treating active leks in jeopardy) and restoration (treating inactive leks with recolonization potential) management across the study area (2.5 million ha) at a total of US$17.5 million, which is within the scope of landscape-level conservation already implemented. An annual investment of US$8.75 million can potentially address encroachment issues near all known Oregon leks within the next decade. Investments in proactive conservation with public and private landowners can increase ecosystem health to benefit species conservation and sustainable land uses, replace top-down regulatory approaches, and prevent conservation reliance of at-risk species.

1. Introduction

Conservation biologists usually argue for a proactive approach to species conservation – making targeted investments before a species is endangered and under substantial risk of extinction (Drechsler et al., 2011; Benson, 2012; Polasky, 2012). But management to abate conservation threats can represent significant investments; globally, annual cost to reduce extinction risk of threatened species was estimated at US$76 billion (McCarthy et al., 2012), and in the U.S., annual cost to protect endangered species from two conservation threats was estimated at US$32 – 42 million (Wilcove and Chen, 1998). Consequently, sufficient action to abate threats starts only when species are under mandated statutory protection to prevent extinction, despite the fact that costs associated with such a reactive delay-and-repair policy may be higher than those of a proactive policy (Scott et al., 2010; Drechsler et al., 2011). Changing policies that direct species conservation from reactive to proactive processes will be one of the major challenges for the conservation community in the coming decades.

In the United States, the Endangered Species Act (ESA) of 1973 is considered as one of the world's strongest legislation providing protection for species of conservation concern (Czech and Krausman, 2001; Taylor et al., 2005; Schwartz, 2008; Harris et al., 2011). Like other conservation policies, the ESA is largely a reactive process. On the eve of its 40th anniversary, over 1400 wildlife and

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plant species were listed as threatened and endangered, and an additional 185 species were designated as candidate for listing (U.S. Fish and Wildlife Service (USFWS), 2013). Candidate status implies there is enough information to warrant protection under the ESA, but listing is precluded because other species are in greater conservation need and therefore receive a higher listing priority (Harris et al., 2011). While candidate species receive no immediate statutory protection, they can provide a unique opportunity to implement proactive management to avoid future listing and prevent them from becoming conservation-reliant species (i.e., requiring continued intervention to maintain viable populations; Scott et al., 2010; Goble et al., 2012).

The greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) is a year-round sagebrush (*Artemisia* spp.) community obligate whose populations have been declining primarily due to habitat loss and fragmentation, which prompted its candidate species designation in 2010 (USFWS, 2010). Key threats leading to sagebrush habitat loss and fragmentation include urbanization and energy development, conversion to croplands, invasion of exotic grasses, large-scale wildfires, and encroachment of conifer species (Knick et al., 2013a). It is estimated that as much as 90% of conifer encroachment in the western U.S. is occurring in sagebrush habitats (Davies et al., 2011; Miller et al., 2011). In its early stages (successional Phase I; Miller et al., 2005), conifer encroachment into sagebrush communities reduces shrub and herbaceous species diversity and increases bare ground (Knapp and Soulé, 1998; Miller et al., 2000). Overtime, trees become co-dominant (Phase II) resulting in the modification of community processes (Miller et al., 2005; Peterson and Stringham, 2008); sagebrush eventually lose vigor and decline in canopy cover, and conifers become the dominant species (Phase III; Miller et al., 2000; Knapp and Soulé, 1998). Miller et al. (2000) documented non-linear declines in sagebrush to approximately 20% of its maximum cover when conifers reached 50% canopy cover. Such losses of sagebrush habitat to conifer encroachment can be detrimental to sagebrush obligate wildlife species, especially those which are already of conservation concern such as the sage-grouse (Knick et al., 2013b; Rowland et al., 2006; Davies et al., 2011).

Previous studies have identified the negative effects of conifer encroachment on sage-grouse by empirically sampling characteristics of used sites (e.g., Freese, 2009; Casazza et al., 2011; Knick et al., 2013a), or by modeling habitat use using the percentage of conifer cover as a covariate (e.g., Doherty et al., 2008; Atamian et al., 2010; Doherty et al., 2010a; but see Casazza et al., 2011). However, there is large variability in stand characteristics as they relate to successional phases after stand establishment (Miller et al., 2005), and understanding how those characteristics affect sage-grouse demographics is essential to target proactive management that is already underway. Launched on the heels of the ESA candidate designation, the Sage Grouse Initiative (SGI) is a collaborative effort between federal and state agencies, non-governmental conservation organizations, and private landowners, to increase ecological understanding, identify critical management needs, and reduce threats to sage-grouse through proactive habitat management (Natural Resources Conservation Service (NRCS) 2013). The SGI implements habitat improvement programs that include acquisition of permanent conservation easements, promotion of sustainable grazing practices, and removal of encroaching conifers (NRCS, 2012), and in the first 2 years of its existence, SGI invested over US$92 million in sage-grouse habitat management. Given such large-scale investments and the immense conservation task at hand, it is important to target SGI's actions to maximize conservation return for every dollar spent.

In this paper we modeled sage-grouse demographics as a function of conifer stand characteristics in eastern Oregon. We demonstrated the application of such analyses to conservation planning by using modeling results to identify areas with high prevention and restoration management potential and to estimate the costs to apply such management. Overall we sought to better understand how conifer stand characteristics relate to sage-grouse demographics to provide guidance for the proactive conservation of this candidate species.

2. Materials and methods

2.1. Study area and lek activity

The study extent consisted of c. 2.5 million ha that were delineated by the NRCS as areas of high management potential and that overlapped current sage-grouse range (Fig. 1). The primary conifer species encroaching into sagebrush habitat in the study area was western juniper (*Juniperus occidentalis*; hereafter juniper), which exhibited geometric growth rates and expanded its range by as much as 600% in the last 150 years (Romme et al., 2009). We eroded (buffered inwards) the study boundaries by the largest scale for which we summarized covariates (5 km), and we included in the analyses data from leks, i.e., breeding sites where males congregate to display to females, that intersected the resulting polygons.

We modeled lek activity as the response variable using yearly peak male lek counts collected by the Oregon Department of Fish and Wildlife (ODFW). Lek activity is an important indicator of population-level impacts because up to 95% of nests are found within 10 km of leks (Holloran and Anderson, 2005; Doherty et al., 2010a; Hagen, 2011), and nest success is a vital rate influencing population growth (Taylor et al., 2012). Since 1996, the ODFW standardized counts as follows: (1) surveys were conducted three times each year during the breeding season (March 15–April 30), (2) lek complexes, defined as group of leks associated with a larger lek in close vicinity (<1.6 km), were completely surveyed in 1 day, (3) repeated lek surveys within a given year occurred at 7–10 day intervals, and (4) counts occurred during the first two hours after daybreak and under clear and calm weather conditions (Hagen, 2011). Following Hagen (2011), we defined leks as active if at least one male was counted within the last 7 years (2005–2011), and as inactive if no males were counted within the same period. Following consultation with ODFW personnel, we considered leks with missing data in the last 7 years as inactive ($n = 29$).

2.2. Conifer mapping and covariates

Spatial wavelet analysis (SWA) is an automated, object-based image analysis method used to map the location and structural properties of trees from high-resolution remotely sensed data (Falkowski et al., 2006; Strand et al., 2006). SWA performs well in characterizing juniper stands with <50% canopy closure (Falkowski et al., 2008; Smith et al., 2008), which is typical of early successional stages associated with conifer encroachment in our study area (Miller et al., 2005). We implemented SWA in program Matlab (2012) to map conifers from an NDVI image derived from 4-band National Agriculture Imagery Program imagery (2009–2010 at 1-m resolution). Specifically, we used a two-dimensional Mexican hat wavelet function and dilated it over a range of potential tree canopy diameters (0–15 m) in 0.1 m increments (Smith et al., 2008). We note that while SWA does not discriminate between juniper and other conifers or deciduous trees, the study area is dominated by western junipers therefore prevalence of other trees is relatively low and likely not to influence interpretation of results.

Because little information was available about the effects of conifer stand characteristics on sage-grouse and the spatial scale at which they operate, covariates were summarized at multiple

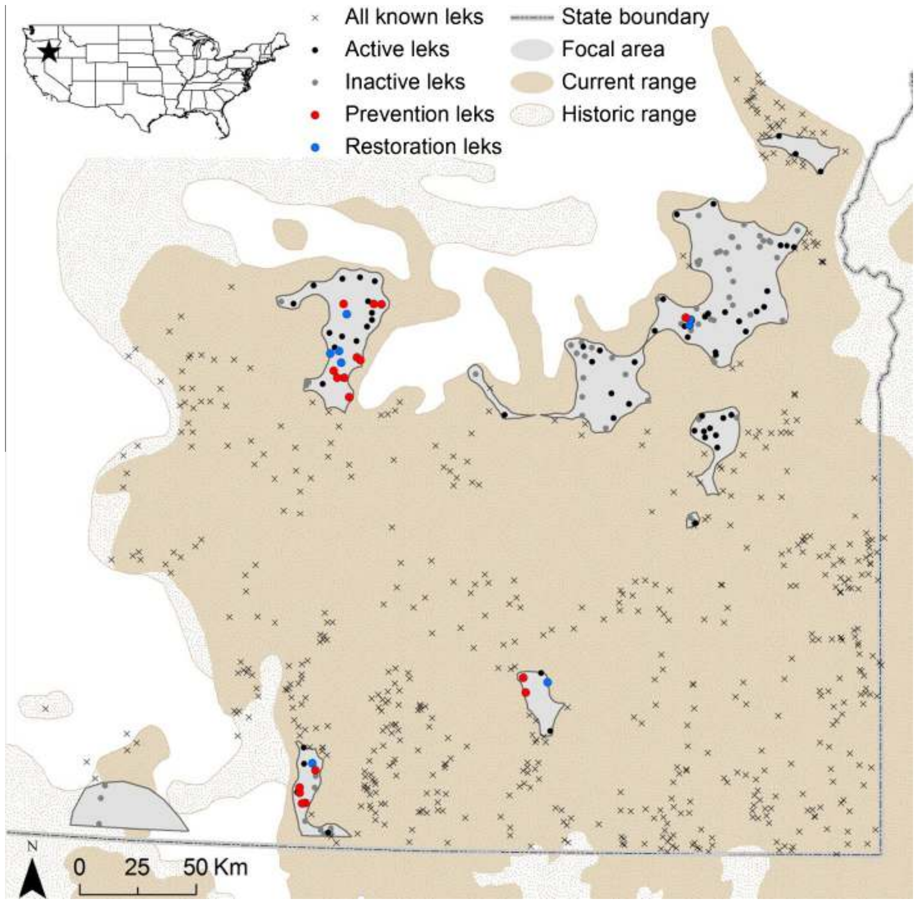

Fig. 1. Outline of the study areas in eastern Oregon, USA, for which tree location and stand characteristics were mapped using high-resolution remote sensing imagery and spatial wavelet analysis. Study area is overlaid with active and inactive greater sage-grouse leks included in modeling analyses, leks with high prevention and restoration potential that were identified using modeling results, all known (active and inactive) Oregon leks monitored since 1941 with at least one count in the last 7 years, and current and historic sage-grouse range are based on Schroeder et al. (2004).

scales from 500 to 5000 m by increments of 500 m, and we retained through model fitting only the scale that explained most variability (analyses performed in program R v. 2.15, R Core Team, 2012). For each lek and scale, we created a circular buffer, intersected the conifer map, and summarized the structural properties of individual trees (crown area), stand configuration (nearest-neighbor index), and landscape cover (percent canopy; Table 1). We produced a probability density function (PDF) of individual crown areas and attributed the function maximum (i.e., most probable value) as crown area (CROWN). We calculated stand configuration (CONFIG) using a nearest-neighbor index (Ebdon, 1985), where values of <1 and >1 respectively correspond to clustered and dispersed tree distributions. Lastly, we used crown areas to calculate percent conifer canopy cover (CONIFER COVER) across the defined scales.

2.3. Additional covariates

Wchile the focus of our analyses was to determine relationships of conifer-related covariates with lek activity, we considered additional covariates relating to lek habitat structure (sagebrush cover and topography), disturbance (anthropogenic disturbance index and fire events), and site productivity (wetness index and climate variables; Table 1). To capture the increasing spatial complexity from the site-specific to landscape-level conditions (Walker et al., 2007; Doherty et al., 2010a), we summarized covariates within a series of buffer distances (500, 1000, 3200, and 5000 m) around each lek.

Leks are typically located in or near sagebrush cover and in relatively flat terrain (Aspbury and Gibson, 2004; Connelly et al., 2011). We summarized proportion of sagebrush canopy cover (SAGEBRUSH) from a 90-m resolution sagebrush cover map (Knick and Connelly, 2011), and we calculated topographic roughness index (ROUGHNESS) as the standard deviation in elevation (Doherty et al., 2008). Anthropogenic infrastructure and activities can negatively affect lek attendance by males (Doherty et al., 2010b; Blickley et al., 2012; Hess and Beck, 2012). We used a human disturbance index (HUMAN) calculated as the proportion of areas classified as agriculture, residential areas, energy development, and roads (Kiesecker et al., 2011). Fire can also negatively affect lek attendance (Connelly et al., 2000); hence we summarized the proportion of burned area (FIRE) based on polygon data available from 1870 to 2007 (Hanser, 2008), but we note that data for fires in our study area spanned only from 1981 to 2005. Because leks are located in close proximity to nesting habitat (Section 2.1), and nesting habitat is positively associated with grass and forb cover (Hagen et al., 200z7; Connelly et al., 2011), we used a wetness index and three climate variables as a surrogate for site potential for grass and forb production. For wetness (WETNESS), we calculated a compound topographic index based on the area of water catchment and topographic slope, where larger values correspond to greater soil moisture (Moore et al., 1991). For other scale-invariant climate covariates, we used normalized 30-year averages from spline climate models (Rehfeldt, 2006) to attribute the mean annual temperature (TEMP), precipitation (PRECIP), and frost-free periods (FROST).

Table 1
Covariates used in the modeling of greater sage-grouse lek activity status. Covariates were summarized within a circular buffer around each lek at scales of 500–5000 m in 500 m increments for conifer-related covariates, and 500, 1000, 3200, and 5000 m for all other covariates except for scale-invariant climate variables (TEMP, PRECIP, and FROST). Scale refers to scale used in final models, importance rank refers to the relative importance of the covariates in random forest modeling, where 1 is the most important covariate, and general trend refers to the smoothed, non-linear, LOWESS trend generated from partial probability plots (Figs. 2 and A1), where x^2 refers to a quadratic relationship. Values at $p = 0.5$ refer to the covariate value(s) corresponding to probability of 0.5.

Name	Abbreviation	Description	Scale (m)	Importance rank	General trend	Value(s) at $p = 0.5$
Conifer						
Crown area	CROWN	The most probable crown area based on a probability distribution function	3000	3	x^2	2.48, 4.20
Stand configuration	CONFIG	Nearest-neighbor index of mapped tree locations; larger values represent more dispersed configuration	5000	9	(−)	0.80
Conifer canopy cover	CONIFER COVER	Percent conifer canopy cover calculated form crown areas	1000	4	(−)	2.00
Lek habitat structure						
Sagebrush cover	SAGEBRUSH	Proportion sagebrush cover	5000	5	(+)	0.81
Topographic roughness index	ROUGHNESS	Standard deviation of elevation; larger values represent increased roughness	5000	1	(−)	9.08
Lek disturbance						
Human disturbance index	HUMAN	Proportion of disturbed pixels from agricultural, residential, energy and road development	5000	2	(−)	0.02
Proportion of fire area	FIRE	Proportion of area within the buffer that experienced a fire event from 1981 to 2005	5000	8	(+)[a]	0.93
Lek site productivity						
Wetness index	WETNESS	Compound topographic index; larger values correspond to higher soil moisture	500	7	(+)	7.19
Mean annual temperature	TEMP			11	(−)	64.08
Mean annual precipitation	PRECIP	Normalized 30-year averages based on spline climate models (Rehfeldt, 2006)	NA	10	(+)	348.01
Frost free period	FROST			6	(−)	92.39

[a] The general positive trend in the smoothed LOWESS curve did not capture a sharp drop in the relative probability of lek activity with an increase of <0.05 in the proportion of area burned (Fig. A1E and F).

2.4. Modeling approach

Random forest (RF) is a weak-learning, ensemble modeling approach based on classification and regression trees (Breiman, 2001; Cutler et al., 2007; Evans, 2011) that is increasingly applied in ecological studies (e.g., Evans and Cushman, 2009; Murphy et al., 2010; Darling et al., 2012). We implemented RF using randomForest package v. 4.6-6 in program R (Liaw and Wiener, 2002), and we modeled lek activity using a two-stage approach. We first ran separate RF models for each of the scale-variant covariates (Table 1) to select for the scale with the highest importance rank (i.e., rank of the relative importance of each covariate), and we then ran a final model that included the selected scales for the scale-variant covariates along with the scale-invariant climate covariates. We ran 5000 trees for each RF model, and we screened covariates for multicollinearity with Variable Inflation Factor (VIF), where we removed variables with VIF > 10 (Dormann et al., 2013). We used model improvement ratio thresholds of 0.1–1 at 0.1 increments for model selection (Murphy et al., 2010), and we iteratively withheld a randomly selected subset of 20% of the data for independent model validation (Evans and Cushman, 2009).

To ensure convergence on selected variables and correct ranking of variable importance, we repeated 1000 iterations of the above procedures, where each iteration was a RF model with 5000 trees (each considered a RF model object), and we averaged results across all iterations. We report the averaged probability, classification errors, and area under the curve (AUC) values, and we combined 100 randomly selected RF model objects (for a total of 500,000 trees) to calculate the predicted global probabilities of activity for active leks in our sample. Finally for display purposes, we present partial probability plots with a smoothed spline function generated with the lowess function in program R (default smoothing parameter of $f = 0.667$). LOWESS graphical methods allow the depiction of the main, non-linear signal in the data (i.e., the general trend of dependency of the response variable on covariate of interest) while smoothing over noise (Cleveland and McGill, 1985).

2.5. Application to conservation planning

We demonstrated the application of modeling results to conservation planning by identifying leks with potential for prevention management (active leks that are in less favorable conifer habitat and are therefore in greater risk of extinction) and for restoration management (inactive leks that are in more favorable conifer habitat and have greater restoration potential), and we estimated the costs to implement management. First, we derived from the predicted LOWESS curves the covariate threshold values associated with a 0.5 probability of lek activity (Table 1). Second, we identified leks with high habitat suitability as those with covariate values ⩽ threshold values where we focused on the top ranking non-conifer-related covariate by category, i.e., habitat structure (ROUGHNESS), disturbance events (HUMAN), and site productivity (FROST) (Table 1; all had general negative trend with probability of lek activity). Third, we independently identified prevention management leks that are in less favorable conifer habitat as active leks with covariate values ⩾ threshold values for CONIFER COVER or CONFIG (negative general trends), or ⩽ lower or ⩾ upper threshold values for CROWN (quadratic general trend). Similarly, we identified restoration management leks in more favorable conifer habitat as inactive leks with values ⩽ thresholds for CONIFER COVER or CONFIG, or ⩾ lower and ⩽ upper thresholds for CROWN. These selection criteria allowed us to site leks with prevention and restoration management potential based on conifer conditions, given that the leks were in otherwise highly suitable habitat as detailed above (i.e., favorable structure, low disturbance, and high productivity).

Once prevention and restoration management leks were identified, we calculated the costs to remove conifers assuming that the average cost is approximately US$250/ha (J. Maestas, personal observation). We note that this is a relatively conservative estimate compared to McClain's (2012) estimate to remove early encroachment stands (US$75/ha) and given that costs vary by tree density, terrain, and degree of post-treatment slash reduction and may only amount to US$62.5/ha (J. Maestas, personal observation). We also note that all cost estimates are based on 2013 US$ values and as currency value change, these estimates may increase or decrease over time. Because each conifer variable was selected at differing scales (Table 1), we estimated the treatment area (ha) around leks (buffer) using radii of 1000, 3000, and 5000 m. For each buffer size, we calculated total costs of conservation as the number of prevention or restoration management leks multiplied by the buffer area multiplied by cost per ha, and we present results rounded to the nearest thousand. Finally, we provided a cost estimate to treat all early encroaching conifer stands (Phase I and II) in Oregon, based on a gross estimate of 354,000 ha within ~5000 m of leks (Maestas and Hagen, 2010).

3. Results

Leks analyzed in this study (n = 152) represented ~20% of all known leks in Oregon with at least one count since 1996 (n = 672), and consisted of 78 active and 74 inactive leks. After screening for multicollinearity and implementing the first-stage RF models, the final RF model included the following: WETNESS at 500 m, CONIFER COVER at 1000 m, CROWN at 3000 m, CONFIG, SAGEBRUSH, ROUHGNESS, HUMAN, and FIRE at 5000 m, and TEMP, PRECIP, and FROST (Table 1). Average model classification errors stabilized quickly and were similar for one-class (36%), zero-class (31%), and out-of-bag data (34%), and average model AUC was 0.67 (SE = 0.0024) across all iterations. The predicted global model probabilities of lek activity for active leks ranged from 0.70 to 0.96.

The habitat structure covariate ROUGHNESS had the highest importance rank, followed by the disturbance covariate HUMAN, and the conifer-related covariate CROWN (Table 1). Disturbance related covariates negatively affected lek activity, and favorable habitat and site productivity covariates positively affected lek activity (Fig. 2, and Appendix A). General trends for top-ranking additional lek covariates were negative for topographic roughness (Fig. 2A) and human disturbance (Fig. 2B), and positive for sagebrush cover (Fig. 2C; plots for rest of covariates in Appendix A). For the conifer-related covariates, lek activity decreased with increasing conifer cover (Fig. 2D) and more dispersed stand configuration (Fig. 2E), and was highest at intermediate crown sizes (Fig. 2F). There were no active leks at conifer cover >4% within 1000 m of lek location.

Further examination of the interaction of clustering (CONFIG) and tree size (CROWN) suggested that the probability of lek activity was higher when tree clustering was high (lower CONFIG values), especially for small crown trees, but was also high for the largest crown sized trees when they were more dispersed (Fig. 3). Mapping stand characteristics for active and inactive leks for a given conifer cover demonstrated that active leks had more clustered trees within their vicinity, and inactive leks had more dispersed distribution of smaller trees, or were completely surrounded by large trees (Fig. 4). That said, we note that there was substantial variability in the data where some active leks persisted in more dispersed stands of smaller trees, and inactive leks were in locations with clustered tree stands.

We identified 17 active leks with prevention management potential and 8 leks with restoration management potential (Fig. 1). For each buffer size, and in increasing order, total costs were

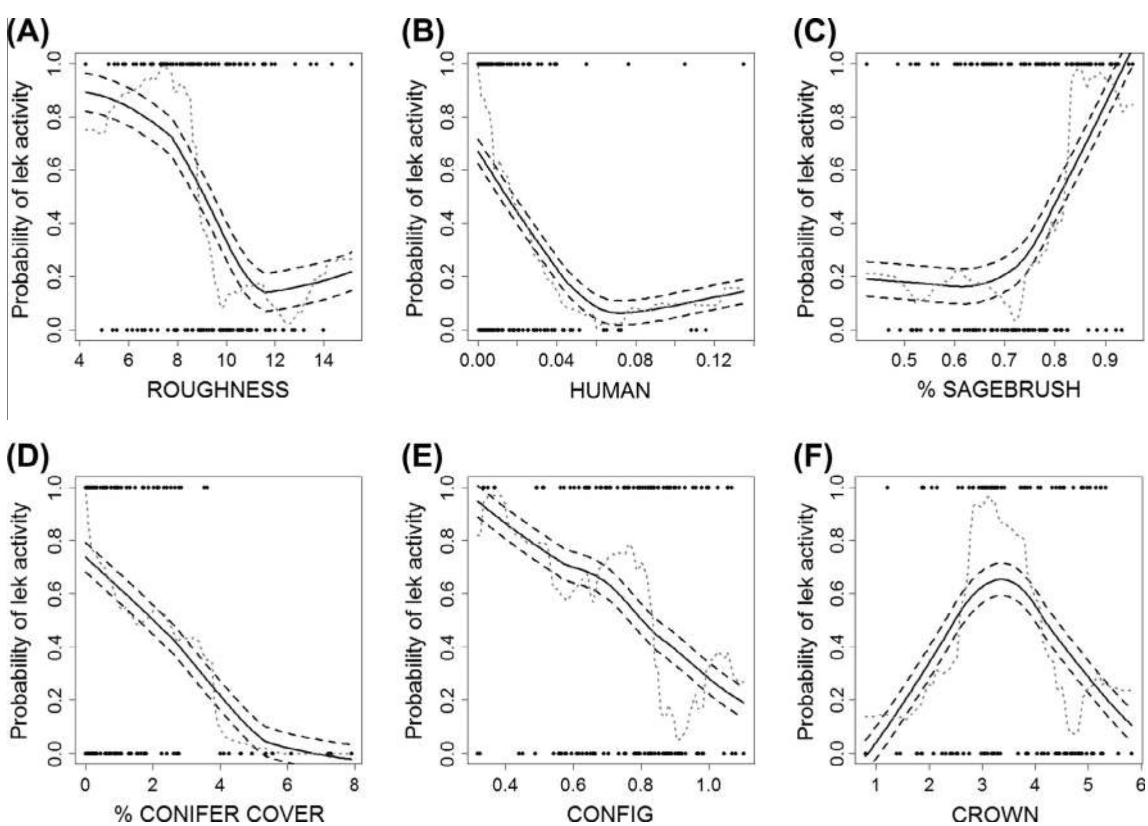

Fig. 2. Partial probability plots (dotted grey), overlaid with LOWESS regression curve (solid black) ± 1.96 SE (dashed black), describing lek activity status as a function of the top three ranking non conifer-related covariates (A–C; Table 1), and of conifer-related covariates (D–F). Partial probability values were averaged over 1000 random forest iterations, each with 5000 trees, and leks activity data are displayed as black dots. See Table 1 for variables' descriptions, scale, and units.

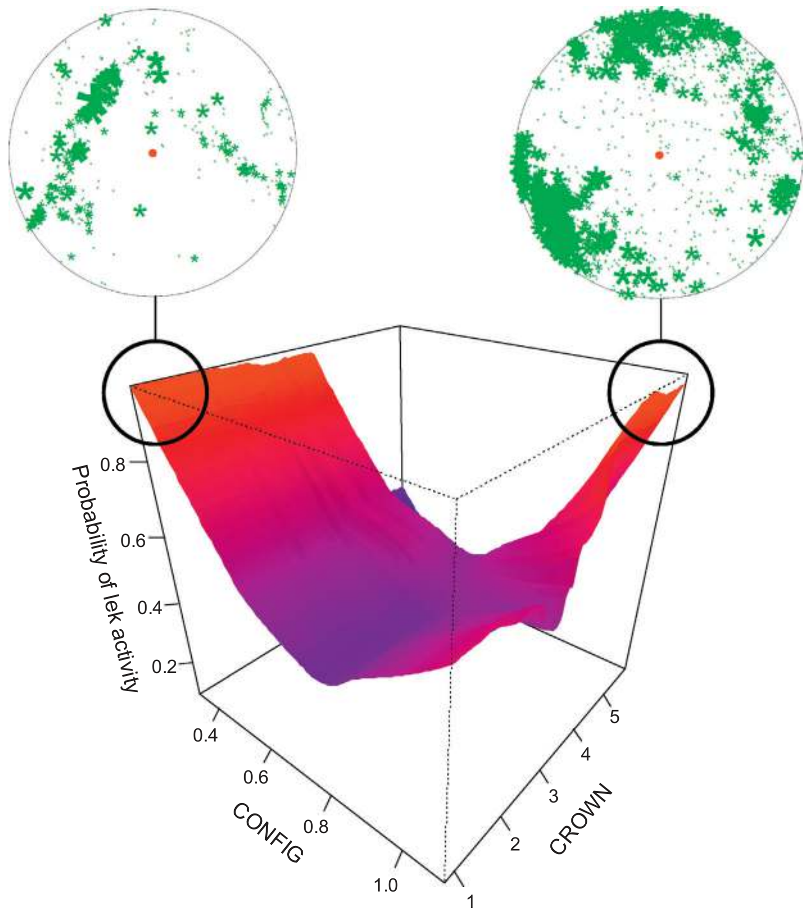

Fig. 3. Perspective partial probability plots of lek activity as a function of conifer crown area (CROWN) and the spatial configuration of trees (CONFIG). Example of stand characteristics associated with high probability areas include high clustering and low crown area (left circle), and low clustering and high crown area (right circle).

US$1,320,000, US$11,877,000, and US$32,993,000 to treat leks with high prevention management potential, and US$621,000, US$5,589,000, and US$15,526,000 for leks with high restoration potential. Total costs to treat all Phase I and II conifer stands within ~5000 m of all leks in Oregon was 87.5 million US$.

4. Discussion

The designation of species as candidate for ESA listing represents an opportunity to implement proactive conservation management to avoid the need for future threatened or endangered listing. A key challenge then becomes how to best target resources to maximize return on limited funds (Drechsler and Wätzold, 2007; Bottrill et al., 2008; McCarthy et al., 2012). Here we demonstrated an approach that links species demographics with detailed attributes of a key conservation threat, and using these developed relationships, also identifies specific sites of high management potential while estimating the required monetary investments.

Conifer encroachment in the Great Basin region is part of ongoing range expansions and contractions in response to prehistoric (Holocene) climate change resulting in increased precipitation (Miller and Wigland, 1994), historic Euro-American settlements that brought about grazing and fire suppression (Miller et al., 2000; Soulé et al., 2004), and more recent (1900s) increases in atmospheric CO_2 levels and precipitation (Miller and Wigland, 1994; Knapp and Soulé, 1998; Knapp et al., 2001). While there is still an active discussion in the literature as to the relative contribution of each factor listed above, authors are generally in agreement that anthropogenic land-use and global climate change synergistically contributed to the recent and rapid range expansion of conifers in the western U.S. (Knapp and Soulé, 1998; Miller et al., 2005; Soulé et al., 2004; Romme et al., 2009; Miller et al., 2011; Baker, 2011). This is especially true in the western U.S., where in the last 150 years conifer species exhibited geometric growth rates and expanded their range by as much as 600% (Romme et al., 2009). Because each factor promoted the expansion and growth of conifer trees at different periods of time (e.g., 1800s, 1900s, etc.), conifer stand characteristics vary across the landscape. Stands of smaller crown and dispersed trees likely represent transitional successional phases of post-settlement expansion, whereas pre-settlement old-growth woodlands typically consist of larger crown trees ranging in configuration from isolated trees on ridges and rocky outcrops to widely scattered trees in sagebrush steppe (Miller et al., 2005). Using SWA we were able to map such detailed stand characteristics, even at very low conifer canopy cover; therefore, we were able to explore how attributes of early successional conifer encroachment stands affect sage-grouse demographics to inform and target proactive conservation.

Our results suggest that sage-grouse incur population-level impacts at a very low level of encroachment as no leks remained active when conifer canopy cover exceeded 4%. This pattern corresponds with other findings of a negative relationship, or avoidance, of conifer habitats during all sage-grouse life stages (i.e., nesting, brood-rearing, and wintering; Doherty et al., 2008; Atamian et al., 2010; Doherty et al., 2010a; Casazza et al., 2011). We note that our results (i.e., AUC of 0.67) suggest that unexplained variability exists, therefore additional monitoring of

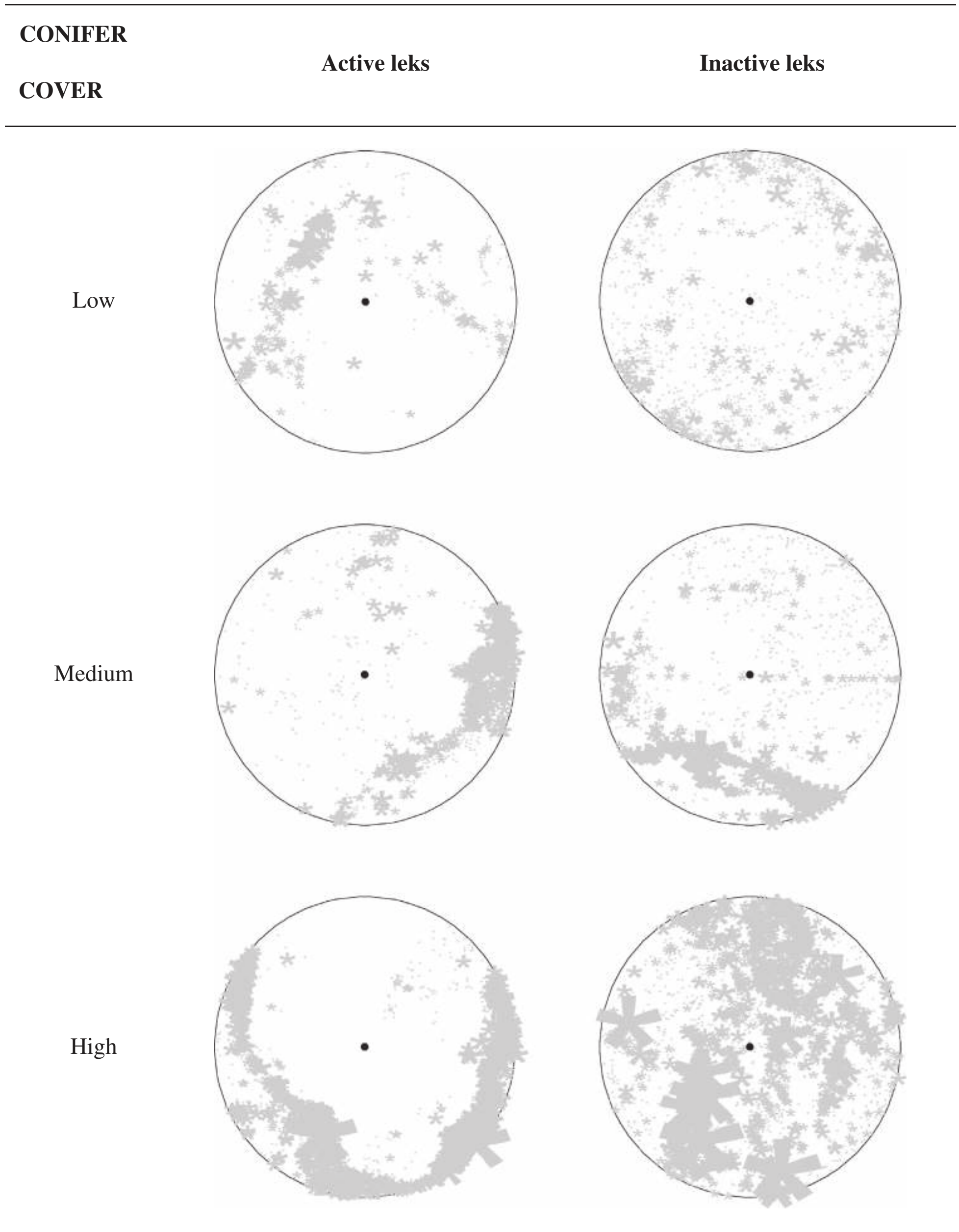

Fig. 4. Examples of stand characteristics within 1000 m of active and inactive leks for a given low (0.33), medium (0.84), and high (2.4) percent conifer cover. Tree crown size is displayed with graduated symbology hence area covered appears larger than actual percent coverage. We note that while we present these leks as visual examples, there was substantial variability in the data and not all areas near active or inactive leks had similar stand characteristics.

sage-grouse population response is needed to further validate the relationships documented in this study. Nevertheless, our ability to capture the spatial configuration and crown size of trees further revealed that for a given conifer canopy cover, whether a lek remained active depended on the spatial configuration of trees (Fig. 4). Leks were more likely to be active where conifer stands were clustered, which is similar in patterns to the fragmenting effects of oil and gas development in which a few leks remained active at clustered well pads configurations (Doherty et al., 2010b). This congruence may indicate a generalized response by sage-grouse to the fragmenting effects of different conservation stressors and could be further explored to potentially generalize management across threats.

The fact that probability of lek activity was predicted to be low where smaller trees were dispersed, or where larger trees were clustered, respectively suggests a negative response of sage-grouse to areas of active encroachment as well as more established stands. Given that established stands are more costly to remove and that no leks remained active at conifer cover of >4%, we recommend initial prioritization of conifer removal investments to Phase I stands, which are characterized by <10% canopy cover and active encroachment (Miller et al., 2005). Miller et al. (2008) estimated that without intervention, 75% of encroachment in the western portion of sage-grouse range may transition into Phase III within the next 30–50 years, thereby placing sagebrush-obligate species at a considerable risk. Currently, the opportunity exists to identify areas for treatment of early Phase II stands to prevent crossing ecological thresholds by the successional transition of sagebrush habitats into conifer woodlands. Such treatment of early phase encroachment is known to be highly effective at maintaining

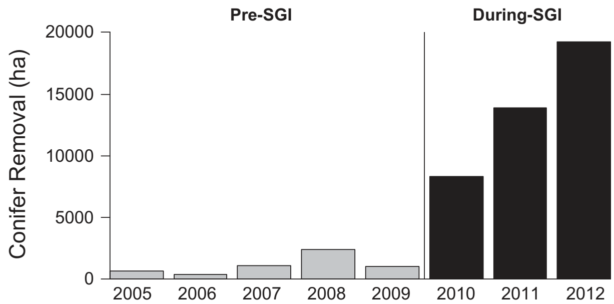

Fig. 5. Total number of annual acres treated for conifer removal in Oregon before and during the Sage Grouse Initiative (SGI).

native shrubs and bunchgrasses, while functionally restoring sagebrush landscapes for 40–50 years on many ecological sites (Davies et al., 2011; Miller et al., 2011).

Using modeling results to identify leks of high prevention and restoration management potential, we were able to fine-tune recommendations and provide a spatially explicit plan for on-the-ground management in eastern Oregon. Because prevention leks are still active, we suggest prioritization of management to prevention leks; however the average distances between prevention (6.7 km) and restoration (4.3 km) leks to the nearest active lek suggest that recolonization of restoration leks post treatment is possible. At the intermediate lek buffer scale for which we estimated costs (3000 m), treating both prevention and restoration leks amounts to the respective management of ~48,000 and 23,000 ha at a collective cost of US$17.5 million. While such investments may seem as formidable costs, they are within the scope of landscape-level conservation already implemented; for example, in the first 3 years of its existence, SGI invested >US$10 million in removing early phase conifer encroachment from >41,000 ha in Oregon alone (Fig. 5). Furthermore, an annual investment of US$8.75 million can potentially address early encroachment issues in breeding habitat near all known Oregon leks over the next decade. Such investments in proactive conservation have the potential to increase both ecosystem health (Davies et al., 2011) and the sustainability of land uses that rely on healthy ecosystems (e.g., livestock ranching; McClain, 2012). A mutually beneficial public-private partnership between land managers and conservationists may serve as a model to replace top-down regulatory approaches with collaborative and proactive solutions for managing at-risk species (Goble et al., 2012).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.08.017.

References

Aspbury, A.S., Gibson, R.M., 2004. Long-range visibility of greater sage grouse leks: a GIS-based analysis. Anim. Behav. 76, 1127–1132.

Atamian, M.T., Sedinger, J.S., Heaton, J.S., Blomberg, E.J., 2010. Landscape-level assessment of brood rearing habitat for greater sage-grouse in Nevada. J. Wildlife Manage. 74, 1533–1543.

Baker, W.L., 2011. Pre-Euro-American and recent fire in sagebrush ecosystems. In: Knick, S.T., Connelly, J.W. (Eds.), Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and its Habitat. Studies in Avian Biology 38. University of California Press, Berkeley, California, USA, pp. 185–201.

Benson, M.H., 2012. Intelligent tinkering: the Endangered Species Act and resilience. Ecol. Soc. 17 (4), 28.

Blickley, J.L., Blackwood, D., Patricelli, G.L., 2012. Experimental evidence for the effects of chronic anthropogenic noise on abundance of greater sage-grouse at leks. Conserv. Biol. 26, 461–471.

Bottrill, M.C., Joseph, L.N., Carwardine, J., Bode, M., Cook, C., Game, E.T., Grantham, H., Kark, S., Linke, S., McDonald-Madden, E., Pressey, R.L., Walker, S., Wilson, K.A., Possingham, H.P., 2008. Is conservation triage just smart decision making? Trends Ecol. Evol. 23, 649–654.

Breiman, L., 2001. Random forests. Mach. Learn. 45, 5–32.

Casazza, M.L., Coates, P.S., Overton, C.T., 2011. Linking habitat selection and brood success in Greater Sage-Grouse. In: Sandercock, B.K., Martin, K., Segelbacher, G. (Eds.), Ecology, Conservation, and Management of Grouse. Studies in Avian Biology 39. University of California Press, Berkeley, California, USA, pp. 151–167.

Cleveland, W.S., McGill, R., 1985. Graphical perception and graphical methods for analyzing scientific data. Science 299, 828–833.

Connelly, J.W., Reese, K.P., Fischer, R.A., Wakkinen, W.L., 2000. Response of a sage grouse breeding population to fire in southeastern Idaho. Wildlife Soc. B 28, 90–96.

Connelly, J.W., Rinkes, E.T., Braun, C.E., 2011. Characteristics of greater sage-grouse habitats: a landscape species at micro- and macroscales. In: Knick, S.T., Connelly, J.W. (Eds.), Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and its Habitat. Studies in Avian Biology 38. University of California Press, Berkeley, California, USA, pp. 69–84.

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

Czech, B., Krausman, P.R., 2001. The Endangered Species Act: History, Conservation Biology, and Public Policy. The John Hopkins University Press, Baltimore, USA.

Darling, E.S., Alvarez-Filip, L., Oliver, T.A., McClanahan, T.R., Côté, I.M., 2012. Evaluating life-history strategies of reef corals from species traits. Ecol. Lett. 15, 1378–1386.

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

Doherty, K.E., Naugle, D.E., Walker, B.L., Graham, J.M., 2008. Greater sage-grouse winter habitat selection and energy development. J. Wildlife Manage. 72, 187–195.

Doherty, K.E., Naugle, D.E., Evans, J.S., 2010a. A currency for offsetting energy development impacts: horse-trading sage-grouse on the open market. PLoS ONE 4, 10339.

Doherty, K.E., Naugle, D.E., Walker, B.L., 2010b. Greater sage-grouse nesting habitat: the importance of managing at multiple scales. J. Wildlife Manage. 74, 1544–1553.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, C., Carré, G., García Marquéz, J.R., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36, 27–46.

Drechsler, M., Wätzold, F., 2007. The optimal dynamic allocation of conservation funds under financial uncertainty. Ecol. Econ. 61, 255–266.

Drechsler, M., Eppink, F.V., Wätzold, F., 2011. Does proactive biodiversity conservation save costs? Biodivers. Conserv. 20, 1045–1055.

Ebdon, D., 1985. Statistics in Geography. Basil Blackwell, Oxford, UK.

Evans, J.S., 2011. Modeling species distribution and change using random forest. In: Drew, C.A., Wiersma, Y.F., Huettmann, F. (Eds.), Predictive Species and Habitat Modeling in Landscape Ecology: Concepts and Applications. Springer, New York, USA, pp. 139–159.

Evans, J.S., Cushman, S.A., 2009. Gradient modeling of conifer species using random forests. Landscape Ecol. 24, 673–683.

Falkowski, M.J., Smith, A.M.S., Hudak, A.T., Gessler, P.E., Vierling, L.A., Crookston, N.L., 2006. Automated estimation of individual conifer tree height and crown diameter via two-dimensional spatial wavelet analysis of lidar data. Can. J. Remote Sens. 32, 153–161.

Falkowski, M.J., Smith, A.M.S., Gessler, P.E., Hudak, A.T., Vierling, L.A., Evans, J.S., 2008. The influence of conifer forest canopy cover on the accuracy of two individual tree measurement algorithms using lidar data. Can. J. Remote Sens. 34, S1–S13.

Freese, M.T., 2009. Linking greater sage-grouse habitat use and suitability across spatiotemporal scales in central Oregon. MS thesis. Oregon State University, Corvallis.

Goble, D.D., Wiens, J.A., Scott, J.M., Male, T.D., Hall, J.A., 2012. Conservation-reliant species. BioScience 62, 869–873.

Hagen, C.A., 2011. Greater Sage-Grouse Conservation Assessment and Strategy for Oregon: a Plan to Maintain and Enhance Populations and Habitat. Oregon Department of Fish and Wildlife.

Hagen, C.A., Connelly, J.W., Schroeder, M.A., 2007. A meta-analysis of greater sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitats. Wildlife Biol. 13, 42–50.

Hanser, S.E., 2008. Western fire map (1870–2007) <http://sagemap.wr.usgs.gov>.
Harris, J.B.C., Reid, J.L., Scheffers, B.R., Wanger, T.C., Sodhi, N.S., Fordham, D.A., Brook, B.W., 2011. Conserving imperiled species: a comparison of the IUCN Red List and U.S. Endangered Species Act. Conserv. Lett. 5, 64–72.
Hess, J.E., Beck, J.L., 2012. Disturbance factors influencing greater sage-grouse lek abandonment in north-central Wyoming. J. Wildlife Manage. 76, 1625–1634.
Holloran, M.J., Anderson, S.H., 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. Condor 107, 742–752.
Kiesecker, J.M., Evans, J.S., Fargione, J., Doherty, K., Foresman, K.R., Kunz, T.H., Naugle, D., Nibbelink, N.P., Niemuth, N.D., 2011. Win–win for wind and wildlife: a vision to facilitate sustainable development. PLoS ONE 6, e17566.
Knapp, P.A., Soulé, P.T., 1998. Recent *Juniperus occidentalis* (western juniper) expansion on a protected site in central Oregon. Glob. Change Biol. 4, 347–357.
Knapp, P.A., Soulé, P.T., Grissino-Mayer, H.D., 2001. Detecting potential regional effects of increased atmospheric CO_2 on growth rates of western juniper. Glob. Change Biol. 7, 903–917.
Knick, S.T., Connelly, J.W., 2011. In: Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and its Habitats. Studies in Avian Biology 38. University of California Press, Berkeley, CA, Online access to GIS products <http://sagemap.wr.usgs.gov/ftp/sab/allsage_90m.zip>.
Knick, S.T., Hanser, S.E., Preston, K.L., 2013a. Modeling ecological minimum requirements for distribution of greater sage-grouse leks: implications for population connectivity across their western range, USA. Ecol. Evol. 3, 1–13.
Knick, S.T., Hanser, S.E., Preston, K.L., 2013b. Modeling ecological minimum requirements for distribution of greater sage-grouse leks: implications for population connectivity across their western range, U.S.A. Ecol. Evol. 3, 1539–1551.
Liaw, A., Wiener, M., 2002. Classification and regression by randomforest. R News 2, 18–22.
Maestas, J., Hagen, C., 2010. Oregon Sage-Grouse Habitat Improvement Initiative: a Strategic Approach to Conservation Program Delivery. USDA Natural Resources Conservation Service.
Matlab, 2012. MATLAB Release 2012b. The MathWorks, Inc., Natick, Massachusetts, United States.
McCarthy, D.P., Donald, P.F., Scharlemann, J.P.W., Buchanan, G.M., Balmford, A., Green, J.M.H., Bennun, L.A., Burgess, N.D., Fishpool, L.D.C., Garnett, S.T., Leonard, D., Maloney, R.F., Morling, P., Schaefer, H.M., Symes, A., Wiedenfeld, D.A., Butchart, S.H.M., 2012. Financial costs of meeting global biodiversity conservation targets: current spending and unmet needs. Science 338, 946–949.
McClain, A., 2012. Ranch level economic impacts of western juniper (*Juniperus occidentalis*) encroachment on sagebrush steppe ecosystems in Owyhee County, Idaho. MS thesis, University of Idaho, Moscow.
Miller, R.F., Wigland, P.E., 1994. Holocene changes in semi-arid pinyon-juniper woodlands: response to climate, fire, and human activities in the US Great Basin. BioScience 44, 465–474.
Miller, R.F., Svejcar, T.J., Rose, J.A., 2000. Impacts of western juniper on plan community composition and structure. J. Range Manage. 53, 574–585.
Miller, R.F., Bates, J.D., Svejcar, T.J., Pierson, B.F., Eddleman, L.E., 2005. Biology, ecology, and management of western juniper. Oregon State University Agricultural Experiment Station Technical, Bulletin 152.
Miller, R.F., Tausch, R.J., McArthur, E.D., Johnson, D.D., Sanderson, S.C., 2008. Age structure and expansion of piñon-juniper woodlands: a regional perspective in the Intermountain West. USDA Forest Service Technical Report: RMRS-RP-69.
Miller, R.F., Knick, S.T., Pyke, D.A., Meinke, C.W., Hanser, S.E., Wisdom, M.J., Hild, A.L., 2011. Characteristics of sagebrush habitat and limitations to long-term conservation. In: Knick, S.T., Connelly, J.W. (Eds.), Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and its Habitat. Studies in Avian Biology 38. University of California Press, Berkeley, California, USA, pp. 145–184.
Moore, I.D., Grayson, R.B., Ladson, A.R., 1991. Digital terrain modelling: a review of hydrological, geomorphological, and biological applications. Hydrol. Process. 5, 3–30.
Murphy, M.A., Evans, J.S., Storfer, A., 2010. Quantifying *Bufo boreas* connectivity in Yellowstone National Park with landscape genetics. Ecology 91, 252–261.
Natural Resources Conservation Service, 2012. Sage-grouse initiative status report fiscal year 2010–2011. <http://www.nrcs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb1047784.pdf> (accessed 09.12).
Natural Resources Conservation Service, 2013. Sage-grouse initiative. <http://www.nrcs.usda.gov/wps/portal/nrcs/detailfull/national/programs/farmbill/initiatives> (accessed 01.13).
Peterson, S.L., Stringham, T.K., 2008. Infiltration, runoff, and sediment yield in response to western juniper encroachment in southeast Oregon. Rangeland Ecol. Manag. 61, 74–81.
Polasky, S., 2012. Conservation in the red. Nature 492, 193–194.
R Core Team, 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Rehfeldt, G.L., 2006. A spline model of climate for the Western United States. Technical Report: RMRS-GTR-165, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. Fort Collins, Colorado, USA.
Romme, W.H., Allen, C.D., Bailey, J.D., Baker, W.L., Bestelmeyer, B.T., Brown, P.M., Eisenhart, K.S., Floyd, M.L., Huffman, D.W., Jacobs, B.F., Miller, R.F., Muldavin, E.H., Swetnam, T.W., Tausch, R.J., Weisberg, P.J., 2009. Historical and modern disturbance regimes, stand structures, and landscape dynamics in piñon-juniper vegetation in the western United States. Rangeland Ecol. Manage. 62, 203–222.
Rowland, M.M., Wisdom, M.J., Suring, L.H., Meinke, C.W., 2006. Greater sage-grouse as an umbrella species for sagebrush-associated vertebrates. Biol. Conserv. 129, 323–335.
Schroeder, M.A., Aldridge, C.L., Apa, A.D., Bohne, J.R., Braun, C.E., et al., 2004. Distribution of sage-grouse in North America. Condor 106, 363–376.
Schwartz, M.W., 2008. The performance of the Endangered Species Act. Annu. Rev. Ecol. Syst. 39, 279–299.
Scott, J.M., Goble, D.D., Haines, A.M., Wiens, J.A., Neel, M.C., 2010. Conservation-reliant species and the future of conservation. Conserv. Lett. 3, 91–97.
Smith, A.M.S., Strand, E.K., Steele, C.M., Hann, D.B., Garrity, S.R., Falkowski, M.J., Evans, J.S., 2008. Production of vegetation spatial-structure maps by per-object analysis of juniper encroachment in multitemporal aerial photographs. Can. J. Remote Sens. 34, S268–S285.
Soulé, P.T., Knapp, P.A., Grissino-Mayer, H.D., 2004. Human agency, environmental drivers, and western juniper establishment during the late Holocene. Ecol. Appl. 14, 96–112.
Strand, E.K., Smith, A.M.S., Bunting, S.C., Vierling, L.A., Hann, D.B., Gessler, P.E., 2006. Wavelet estimation of plant spatial patterns in multitemporal aerial photography. Int. J. Remote Sens. 27, 2049–2054.
Taylor, M.F.J., Suckling, K.F., Rachlinski, J.J., 2005. The effectiveness of the Endangered Species Act: a quantitative analysis. BioScience 55, 360–367.
Taylor, R.L., Walker, B.L., Naugle, D.E., Mills, L.S., 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. J. Wildlife Manage. 76, 336–347.
USFWS, 2010. Endangered and Threatened Wildlife and Plants; 12-month findings for petitions to list the greater sage-grouse (*Centrocercus urophasianus*) as threatened or endangered; proposed rule. Fed. Register 75, 13910–14014.
USFWS, 2013. Endangered Species Program – Species lists. <http://www.fws.gov/endangered/> (accessed 01.13).
Walker, B.L., Naugle, D.E., Doherty, K.E., 2007. Greater sage-grouse population response to energy development and habitat loss. J. Wildlife Manage. 71, 2644–2654.
Wilcove, D.S., Chen, L.Y., 1998. Management costs for endangered species. Conserv. Biol. 12, 1405–1407.