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Next-generation restoration for sage-grouse: a framework for visualizing local conifer cuts within a landscape context

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Abstract. The expansion of coniferous trees into sagebrush ecosystems is a major driver of habitat loss and fragmentation, resulting in negative impacts to wildlife. Greater sage-grouse (*Centrocercus urophasianus*) respond directly to conifer expansion through decreased breeding activity, nesting, and overall survival; thus, small amounts of conifer expansion can have significant impacts on sage-grouse habitat and populations. To this end, conservation partners have collaborated across private and public lands to reduce the threat of conifer expansion through targeted removal of conifer trees. Here, we demonstrate the use of the Marxan framework to incorporate important ecosystem attributes in the prioritization of conifer removal within the Oregon range of sage-grouse. We prioritized conifer removal relative to three separate goals: (1) enhancement of existing sage-grouse breeding, nesting, and early brood-rearing habitats; (2) facilitation of sage-grouse movement between breeding and brood-rearing habitats; and (3) improvement of connectivity among sage-grouse priority areas for conservation (PACs). Optimization models successfully identified areas with low conifer canopy cover, high resilience and resistance to wildfire and annual grass invasion, and high bird abundance to enhance sage-grouse habitat. The inclusion of mesic resources resulted in further prioritization of areas that were closer to such resources, but also identified potential pathways that connected breeding habitats to the late brood-rearing habitats associated with mesic areas. Examining areas outside of PACs resulted in the selection of potential corridors to facilitate connectivity; although areas with low conifer cover were selected similarly to the other optimization models, areas with high cover were also chosen to be able to enhance connectivity. Areas identified by optimization models were largely consistent with and overlapped ongoing conifer removal efforts in the Warner Mountains of south-central Oregon. Land ownership of preferential areas selected by models varied with priority goals and followed general ownership patterns of the region, with public lands managed by the Bureau of Land Management and private lands being selected the most. The increased availability of landscape-level datasets and assessment tools in sagebrush ecosystems can reduce the time and cost of both planning and implementation of habitat projects involving conifer removal. Most importantly, incorporating these new datasets and tools can supplement expert-based knowledge to maximize benefits to sagebrush and sage-grouse conservation.

Key words: conifer; juniper; landscape; Marxan; optimization; pinyon; sage-grouse.

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Introduction

Conservation and restoration needs often exceed funding and human capacity (James et al. 1999, see also Bottrill et al. 2008), so strategically targeting resources to optimize desired outcomes is critical. This is traditionally accomplished using local and expert knowledge (Prendergast et al. 1999), spatially explicit models (e.g., Johnson et al. 2004), and increasingly, systematic planning approaches (Margules and Pressey 2000). Systematic approaches are particularly useful because they allow for the integration of multiple data types as well as the consideration of multiple, potentially competing, objectives (e.g., multiple species, different lifecycle stages, etc.). This flexibility is especially valuable in systems with several key considerations, for example, species of conservation concern, invasive species, and significant seasonal and environmental variation. Here, we focus on the potential utility of using a systematic site selection approach for one such example: targeting the removal of expanding conifers in sagebrush (*Artemisia* spp.) ecosystems in Oregon, USA.

Sagebrush systems once dominated over 620,000 km^2 across the western United States (McArthur and Plummer 1978, Miller et al. 1994). Today, these ecosystems have been reduced to nearly half of their former distribution (Knick et al. 2003) due to a wide array of stressors, including conifer expansion (Miller and Rose 1999, Knick et al. 2013). Native juniper (*Juniperus* spp.) and pinyon pine (*Pinus edulis*, *Pinus monophylla*) woodlands have expanded by 625% (Miller and Tausch 2001, Miller et al. 2011) largely at the expense of sagebrush ecosystems (Miller et al. 2011). This expansion is primarily the result of fire suppression and heavy historic grazing activities associated with European settlement during the late 19th century (Miller and Rose 1999). Conifer expansion alters ecosystem structure and function (Miller et al. 2005, Pierson et al. 2010, Davies et al. 2011, Kormos et al. 2017), resulting in negative impacts on sagebrush-obligate wildlife species (Connelly et al. 2000, Miller et al. 2017).

The greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) is a large galliform bird native to sagebrush ecosystems across the western United States. Fragmentation and loss of sagebrush ecosystems has reduced by half the sage-grouse-occupied range (Schroeder et al. 2004). Indeed, the corresponding decline in sage-grouse numbers has led to consideration of federal protections for the species under the U.S. Endangered Species Act. In 2015, the U.S. Fish and Wildlife Service (USFWS) found the sage-grouse "not-warranted" for listing due to ongoing conservation efforts and partnerships, but that decision is scheduled for additional review in 2020 (USFWS 2015). Thus, proactive land management strategies that benefit sage-grouse are of interest to a number of parties, including private landowners, public land management agencies, and conservation organizations.

A plethora of conservation issues face sage-grouse including anthropogenic development (e.g., Swenson 1987, Holloran 2005, Naugle et al. 2011, Blickley et al. 2012, Gregory and Beck 2014, Kirol et al. 2015, Hansen et al. 2016), large-scale wildfire (Nelle et al. 2000, Coates et al. 2017), and invasive species (e.g., Chambers et al. 2007, Davies and Svejcar 2008). However, the issue of conifer expansion is of particular interest due to the apparent sensitivity of sage-grouse to even small amounts of conifer cover in sagebrush communities. Baruch-Mordo et al. (2013) found that sage-grouse breeding grounds, or leks, became inactive even at very low (4%) levels of conifer canopy cover. Severson et al. (2017*a*) confirmed this finding at local scales showing that nesting sage-grouse hens avoided otherwise suitable habitat with >3% conifer cover. Additional evidence from Prochazka et al. (2017) across 12 Great Basin study sites documents faster movements and lower survival of sage-grouse, especially in juvenile birds, when navigating conifer-invaded sagebrush systems. Their findings identify a behavioral mechanism in which pinyon–juniper expansion decreases sage-grouse habitat suitability. These studies suggest that even relatively small amounts of conifer expansion into sagebrush ecosystems could translate into significant reductions in sage-grouse habitat availability and potentially result in population-level impacts.

To address the conifer expansion threat, conservation partners across private and public lands have greatly accelerated conifer removal (USFWS 2015) across seasonal habitats. Sage-grouse leks are frequently used in prioritization of conifer treatments because their locations are widely available and the landscape surrounding them often serves as a reasonable surrogate for core habitat areas (Fedy et al. 2012). Targeting conifer removal around leks is thought to give managers a relatively high biological return for their financial investment (SGI 2016) because it has been shown to increase usable habitat space for sage-grouse near sensitive breeding, nesting, and early brood-rearing areas (Frey et al. 2013, Sandford et al. 2017, Severson et al. 2017*a*). There are, however, other valuable ecosystem characteristics—beyond leks—to consider while prioritizing conifer removal treatments across the sagebrush biome. Recent work (Atamian et al. 2010, Dahlgren et al. 2016, Donnelly et al. 2016) has highlighted the importance of late-season brood-rearing (hereafter "late brood-rearing") habitats that can also be prone to conifer expansion impacts (Bates et al. 2017). By late summer (July–August), warmer temperatures and seasonal drying cause hens and broods to seek more productive, mesic habitats for forb and insect food resources (Fischer et al. 1996, Connelly et al. 2011, Dahlgren et al. 2016, Donnelly et al. 2016). Conifer expansion may inhibit, or increase the risk associated with, seasonal movement of sage-grouse (Beck et al. 2006, Coates et al. 2017, Prochazka et al. 2017). As a result, removing trees to facilitate bird movement between breeding and late brood-rearing habitats is gaining interest as a potential management strategy (e.g., Dahlgren et al. 2016). Finally, because sage-grouse are widely spread across their historic range (Knick and Connelly 2011), there has also been a growing interest in facilitating connectivity at landscape to regional scales (Knick et al. 2013, Crist et al. 2017). This connectivity could be a potentially important conduit for maintaining gene flow and may help to mitigate regional threats to sage-grouse (Knick et al. 2013, Cross et al. 2016).

To better prioritize management efforts at the landscape scale, sage-grouse priority areas of conservation (PACs) were delineated by the state wildlife agencies and U.S. Fish and Wildlife Service. These areas represent strongholds needed to support species persistence (USFWS 2013). Priority areas of conservations provide an important biological tool to focus management efforts (SGI 2016), but the ability to evaluate specific threats like conifer expansion in relation to PACs has been limited by a lack of detailed datasets and landscape assessment tools. However, a recently developed high-resolution conifer prediction map (Baruch-Mordo et al. 2013, Falkowski et al. 2017) provides a synoptic view of threats across the sage-grouse range, thus allowing a more nuanced assessment of management actions. Although this new mapping shows a high proportion of expanding conifer plants at a low to intermediate canopy cover, providing context and time for management intervention, a systematic approach that maximizes the biological return on investment is lacking.

Here, our goal was to provide a demonstrative framework that could help local land managers determine where prime conifer removal locations occur on a landscape, and why those locations might be considered optimal. To that end, we employed a systematic landscape optimization approach to identify potential conifer removal locations based on the estimated benefit to sage-grouse across a number of competing factors encompassing the bird's lifecycle, habitat connectivity, policy, and management objectives. This approach is highly adaptable because it allows for the incorporation of both large-scale (e.g., ecological patterns) and small-scale (e.g., local management objectives) attributes in the optimization. It also easily accommodates a collaborative scoping process where stakeholder input can lead directly to actionable coproduced science (e.g., Beier et al. 2016). Our specific objective was to employ such a systematic planning approach to identify, within the Oregon sage-grouse range, the most important areas for conifer removal that would (1) enhance existing sage-grouse breeding, nesting, and early brood-rearing habitats; (2) facilitate movement between sage-grouse breeding and late brood-rearing habitats; and (3) improve connectivity pathways among sage-grouse PACs at the landscape scale. Following the optimization, we explored differences in the distribution of potential (targeted) conifer removal areas across land ownership and compared our results with recent management efforts in the Warner Mountains of south-central Oregon.

Methods

Study area

This study focused on the sage-grouse range within eastern Oregon (Fig. 1). The region is

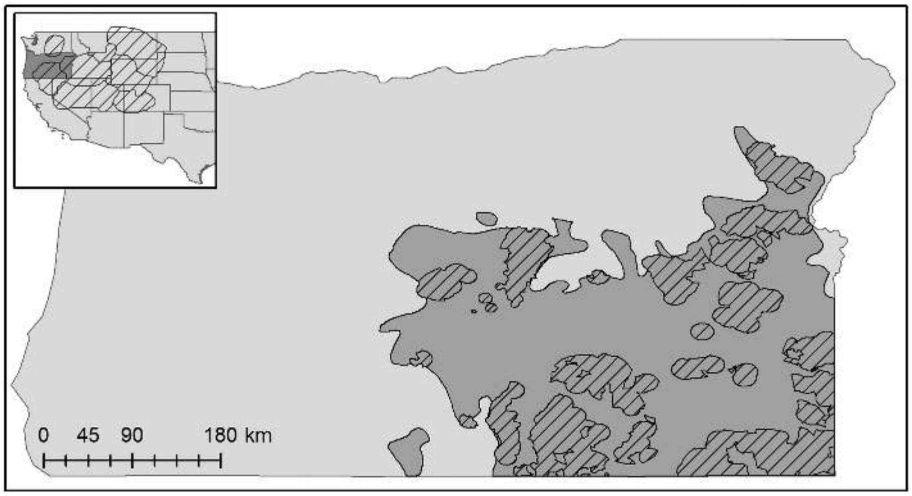

Fig. 1. Oregon, USA. Study area highlighted in dark gray. Sage-grouse priority areas of conservation highlighted with black crosshatched polygons. Inset: sage-grouse management zones (hatched polygons) over the western USA, Oregon, highlighted.

characterized by lava plains and basin-range topography. Eastern Oregon has a semi-arid continental climate, which averages 318 mm of precipitation per year (1901–2000; NOAA 2016). The average (1901–2000) winter temperature (Dec–Feb) ranges from −10° to 6°C, and the average summer (Jun–Aug) temperature ranges from 10° to 24°C (NOAA 2016). Sagebrush (*Artemesia* spp.) steppe dominates much of the region, followed by conifer (*Juniperus*, *Pinus*, *Abies* spp.) forests and woodlands. This region has been a focal point for sage-grouse conservation and management, with over 20,000 ha of conifer removal efforts in the last three years (SGI 2016). The ongoing interest in sage-grouse conservation and conifer management makes this an ideal area for developing a landscape optimization approach to target ongoing conifer removal.

Data

To identify the most important areas for conifer removal, we used a simulated annealing algorithm implemented via the Marxan framework (Ball et al. 2009). This required a number of geospatial datasets relating to conifer cover, sage-grouse, and sagebrush ecosystems. First, we leveraged a recently developed high-resolution conifer cover prediction map (Baruch-Mordo et al. 2013, Falkowski et al. 2017). The conifer mapping process estimates canopy cover via an image processing approach called spatial wavelet analysis (SWA; Falkowski et al. 2006) executed on four-band, 1-m spatial resolution National Agricultural Imagery Program (NAIP) data. Spatial wavelet analysis allows for the identification of individual trees on the landscape and an estimation of their crown size. From these location and size estimates, a reclassified canopy cover map was created for our entire study area based on 2011 NAIP data. The methods used to create this dataset are described in detail by Poznanovic et al. (2014) and Falkowski et al. (2017); full dataset can be visualized and downloaded at http://map.sagegrouseinitiative.com/.

Sage-grouse lek locations were used as indicators of active breeding habitat locations. Lek survey data were obtained from the Oregon Department of Fish and Wildlife for the years 2005–2015 (ODFW 2015). Lek locations and their adjacent areas were represented using two concentric buffers, which were assigned a quantitative value based on their sage-grouse breeding population size and distance from lek center (i.e., buffer distance); leks were given full weight up to a distance of 1 km, and half-weight up to a distance of 4 km; these distances were chosen based on lek and bird data presented in previous and ongoing work (Severson 2016, Severson et al. 2017*a*). We also leveraged a sage-grouse breeding habitat distribution model constructed by

Doherty et al. (2016) to serve as a continuous representation of sage-grouse breeding habitat suitability. This model was constructed using a random forest approach, based on 20 environmental variables (from 2008 to 2014) encompassing vegetation and coarse canopy cover, hydrology, climate, physiography, and disturbance regimes (Doherty et al. 2016). Sagebrush cover data were obtained from a moving-window analysis of LANDFIRE v1.3.0 data (LANDFIRE 2012). As an indicator of potential sagebrush ecosystem productivity and likelihood of favorable vegetation response post-treatment, we used a recently described index of resilience to disturbance and resistance to invasive annual grasses (hereafter R&R) derived from abiotic factors that heavily influence vegetation (Maestas et al. 2016).

Given the importance of mesic habitats for seasonal sage-grouse brood rearing (Atamian et al. 2010, Dahlgren et al. 2016, Donnelly et al. 2016), we were interested in identifying potential pathways that would facilitate movements between breeding habitat (leks) and late-season mesic resources. We incorporated a mesic resources dataset constructed by Donnelly et al. (2016) that used a Normalized Difference Vegetation Index analysis of Landsat imagery (1984–2011; Landsat 4–5) to identify distinct mesic resources that remained productive during late summer. To help identify areas where conifer removal could facilitate movements between sage-grouse breeding and brood-rearing habitats, we created a raster that describes the relative distances between lek locations and the mapped mesic resources.

We were also interested in identifying areas where conifer removal efforts might facilitate connectivity between sage-grouse populations at the landscape scale. To address this objective, we used a resistance surface analysis (Circuitscape; McRae 2006) of habitat similarity indices constructed by Knick et al. (2013). By treating the landscape as a "conductive surface" and potential animal movement and populations as "current," Knick et al. (2013) created a spatially explicit representation of bird movement potential across the sage-grouse range. This movement potential provides important context for identifying areas where removing conifers could improve connectivity between sage-grouse populations. Finally, we also computed a simple between-PAC distance raster to highlight the most direct pathways between delineated priority areas.

Analysis

All spatial data were aggregated by averaging across a grid of 30-hectare (340 m per side) hexagon polygons using the zonal statistics tool in ArcGIS 10.2. This hexagonal resolution was chosen based on preliminary analyses and discussions with stakeholders. Using this grid, we applied a simulated annealing algorithm with iterative improvement to identify potential areas for conifer removal. The algorithm was implemented using the Marxan R package (Hanson and Watts 2015, R Core Team 2016; see also Ball et al. 2009). Marxan is a conservation decision support tool originally developed to help inform the design of reserves and protected areas (Ball et al. 2009). Marxan is able to provide a near-optimal solution for either a minimum set or maximum coverage problem (see Ball et al. 2009). In a conservation context, minimum set problems seek to meet conservation goals while minimizing costs, while maximum coverage problems seek to maximize conservation variables under a fixed cost threshold. Marxan finds solutions for these problems using algorithms such as simulated annealing (used herein). Variables to be maximized in the algorithms are typically referred to as conservation features, and are generally offset by a cost term (Ball et al. 2009, Ardron et al. 2010).

In this case, we used a variety of sage-grouse-related data as conservation features (Table 1). Categorical variables of conifer cover (1–5%, 6–10%, 11–20%, 21–50%, >50%) and R&R (High, Medium, Low) were used additively as a cost factor, such that a high (>50%) canopy cover hexagon with "Low" resilience would have the highest cost. Hexagons that had no conifer cover were excluded from analyses as they contained no conifer to prioritize for removal. We set proportional optimization targets of 0.3 for each conservation feature, and we used a boundary length modifier of 0.001, which we found to balance solution costs and area with boundary length (see Ardron et al. 2010). The algorithm was configured for 10 million iterations across 1000 runs; increasing iterations and runs beyond these numbers in preliminary analyses had no appreciable impact on the results. We used final

Table 1. Summary of data included in each simulated annealing model.

Data	Breeding habitat enhancement	Seasonal movement	Between-PAC connectivity
Area of interest	PACs	PACs	Between PACs
Lek data	×	×	×
Sagebrush cover	×	×	×
Breeding habitat suitability model	×	×	
Lek-to-mesic habitat		×	
Movement potential (connectivity)			×
Between-PAC pathways			×

Notes: PAC, priority areas of conservation. Descriptions and sources for each data layer are provided in text. × indicates that the variable was included in that particular model.

selection frequency ("sf"; i.e., proportion of runs in which a particular hexagon cell was included as a solution in the algorithm) as an indicator of irreplaceability, or "importance level" for conifer removal (Carwardine et al. 2007, Ardron et al. 2010). Importance categories were developed to simplify visualization of results; hexagons were split into four groups based on their sf: groups 1 (sf > 0.95), 2 (sf 0.67–0.95), 3 (sf 0.33–0.66), and 4 (sf < 0.33).

We ran three optimization models matched to objectives described above. First, to identify potentially important conifer removal areas that would enhance existing breeding habitat, we incorporated sage-grouse lek data (as weighted buffers), sagebrush cover, and the breeding habitat suitability model as conservation features. Our second model sought to identify conifer removal areas that would improve seasonal habitat movement, so we incorporated our breeding–brood-rearing habitat layer as a conservation feature (Table 1). These first two models, "breeding habitat enhancement" and "seasonal movement," were both computed within PACs.

Our third model identifies potential areas for conifer removal that would enhance landscape-level connectivity between PACs. To that end, we included the landscape-level sage-grouse movement potential data (Knick et al. 2013) and a between-PAC corridor layer as conservation features (Table 1). For the between-PAC connectivity model, we considered only the portion of the study area located between PACs, the inverse area of interest from the previous two models. The breeding habitat distribution dataset (Doherty et al. 2016) was excluded as input for the between-PAC connectivity model, as the sage-grouse movement potential dataset (Knick et al. 2013) was constructed based on similar habitat data.

Selection frequency was mapped across all models and summarized using kernel density plots. We compared the breeding habitat enhancement with the seasonal movement models, both of which were run only within PACs, using a Kolmogorov-Smirnov test and a linear model. For all models, we compared distribution of importance groups across different ownerships using summary tables.

Lastly, in order to assess how our models were compared to ongoing management efforts, we compared our Marxan output to conifer removal activities in the Warner Mountains of south-central Oregon, one of the largest-scale and ongoing restoration efforts in the west (Severson et al. 2017*a*). Output for the breeding habitat enhancement and seasonal movement models was compared with conifer removal efforts that occurred in the years 2011–2014. Because our models are built around a 2011 SWA conifer cover dataset, this selection of years allowed us to assess how conifer removal efforts matched up with our results.

Results

Breeding habitat enhancement and seasonal movement optimization models targeted conifer removal across 2.6 million ha of land within PACs, while our between-PAC optimization model spanned 4.9 million ha of between-PAC area. Findings were broadly consistent, with most hexagon cells having a sf < 0.1 across all three optimization models (Fig. 2). The breeding habitat enhancement model demonstrated relatively higher selection frequencies between 0.7 and 1.0, with relatively fewer between 0.2 and 0.6 (Fig. 2). In contrast, the seasonal movement model exhibited high selection frequencies between 0.2 and 0.5, and very low frequencies between 0.6 and 0.8 (Fig. 2). This difference highlights the role of

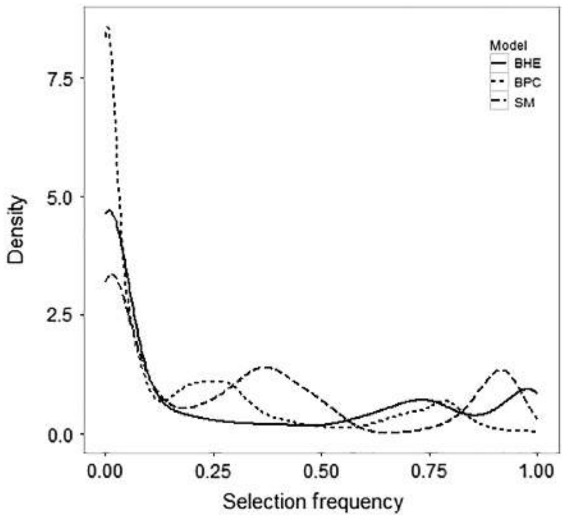

Fig. 2. Kernel density plot of hexagon selection frequency by model. BHE, breeding habitat enhancement; BPC, between- priority areas of conservation connectivity; SM, seasonal movement.

movement pathways between seasonal habitats on the optimization algorithm; while there was a coarse linear relationship ($r^2 = 0.74$) in overall sf between models, inclusion of mesic resources meaningfully altered structure of the sf distribution (K-S test: $P < 0.001$, $D = 0.211$; Fig. 2).

Selection frequency was heavily left-skewed in the between-PAC connectivity model (Fig. 2). Most hexagons were not selected at all, either due to a failure to meet model selection criteria (i.e., they contained too few of our desired conservation features) or due to a lack of conifer cover to be considered for removal. Hexagons that were selected by the between-PAC connectivity model were generally located along pathways between PACs (e.g., Fig. 6), especially where sage-grouse movement potential was highest (as assessed by Knick et al. 2013).

Distribution of potential areas for conifer removal across land ownership was broadly similar for all three optimization models, with a few notable differences. In general, the highest proportions of selected hexagons were located on lands owned by the U.S. Bureau of Land Management (BLM; >0.6) or privately owned ranches (>0.2; Table 2). This result largely reflects ownership patterns in the region (Appendix S1: Tables S1 and S2). We found a higher proportion of medium-high importance (s.f. > 0.33) hexagons situated on private lands in the seasonal movement model as compared to the habitat enhancement model (0.046 vs. 0.029; Table 2; Appendix S1: Table S3), likely due to the known private ownership of mesic resources (Donnelly et al. 2016).

Ongoing conifer removal efforts overlap to varying extents with our breeding habitat enhancement and seasonal movement models (Figs. 3, 7). On-the-ground removal efforts in the Warner Mountains in Oregon appear to be tracking the seasonal movement model output more closely than the habitat enhancement model based on the distribution of medium-high importance hexagons across conifer treatment areas over time

Table 2. Distribution of model selection frequency (sf) classes across ownerships, as a proportion of total.

Ownership	sf Class	BLM	Private	State	USFS	USFWS
Breeding habitat enhancement	<0.33	0.638	0.205	0.033	0.009	0.031
	0.34–0.66	0.015	0.005	0.001	0.000	0.000
	0.67–0.95	0.020	0.014	0.001	0.001	0.003
	0.96–1.0	0.014	0.010	0.000	0.000	0.001
Seasonal movement	<0.33	0.627	0.186	0.032	0.008	0.030
	0.34–0.66	0.040	0.021	0.001	0.001	0.003
	0.67–0.95	0.023	0.022	0.000	0.001	0.002
	0.96–1.0	0.001	0.003	0.000	0.000	0.000
Between-PAC connectivity	<0.33	0.589	0.270	0.024	0.039	0.017
	0.34–0.66	0.019	0.006	0.001	0.001	0.000
	0.67–0.95	0.020	0.014	0.001	0.001	0.000
	0.96–1.0	0.001	0.000	0.000	0.000	0.000

Notes: BLM, Bureau of Land Management; USFWS, U.S. Fish and Wildlife Service. Higher sf classes indicate prioritization for conifer management.

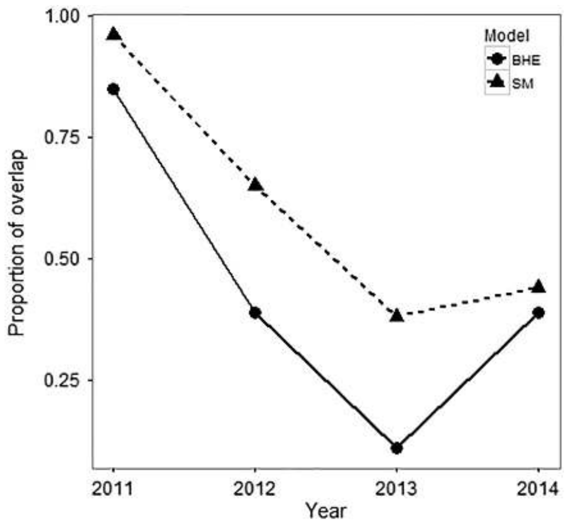

Fig. 3. The proportion of overlap, by year, between already implemented conifer treatment plots in the Warner Mountains and breeding habitat enhancement (BHE) and seasonal movement (SM) optimization model outputs. Only hexagons with a model selection frequency >0.33 were considered.

(Fig. 3). We also find that the proportion of overlap between model output hexes with selection frequencies >0.33 and on-the-ground conifer removal efforts decreases over time from a high of over 0.8 in both models in 2011, to ~0.4 by 2014, and a low of 0.05 for the breeding habitat enhancement model in 2013 (Fig. 3). This pattern may be a result of managers choosing more "optimal" areas for conifer removal first.

Discussion

Newly developed landscape assessment tools including high-resolution conifer (Baruch-Mordo et al. 2013, Poznanovic et al. 2014, Falkowski et al. 2017) and mesic resource (Donnelly et al. 2016) mapping enabled us to develop the first landscape models that optimize benefits of conifer removal to sage-grouse across multiple life history phases (Fig. 4). Our optimization framework helps practitioners to visualize their local management decisions within a landscape context and enables them to anticipate whether future actions are most likely to benefit breeding, late brood rearing, or between-PAC connectivity. Our optimizations come at a time in the history of sage-grouse management when a myriad of new studies support a landscape approach to reduce conifer encroachment (Miller et al. 2017). New science has spurred an unprecedented call from practitioners for frameworks that biologically justify next-generation cuts knowing that if done right, individual efforts will accumulate into landscape-level benefits to grouse and the larger sagebrush ecosystem. We do not desire or anticipate that practitioners will blindly apply our optimizations within their local watersheds; instead, our findings provide a potential pathway for considering and incorporating landscape conservation into decisions that still allow room for social acceptance within the local community.

Our breeding habitat enhancement model preferentially selected future cuts within high bird abundance PACs with lower conifer canopy cover and higher R&R scores (Fig. 4). Recent literature supports conifer removal during early stages of woodland succession on higher R&R sites because management is more likely to produce desired vegetation responses since native understory herbaceous and shrub communities are often intact and risk of exotic annual grass expansion following removal is lower (Miller et al. 2014, Roundy et al. 2014). Identifying these locations on the landscape may be particularly relevant given recent work showing that these areas may function as ecological traps, in which sage-grouse continue using otherwise productive areas with low tree cover but suffer lower survival (Coates et al. 2017). Given the importance of female survival, nest success, and chick survival to sage-grouse population demographics (Taylor et al. 2011), improving existing breeding, nesting, and early brood-rearing habitats by creating more usable space around leks is now an elevated conservation priority (Frey et al. 2013, Sandford 2016, SGI 2016, Severson et al. 2017*a, b, c*). Removing conifer cover around existing breeding habitat may increase lek persistence (Baruch-Mordo et al. 2013, see also Aldridge et al. 2008), nesting habitat availability and space use (Sandford et al. 2017, Severson et al. 2017*a*), and potentially bird abundance (Commons et al. 1999, Severson et al. 2017*c*).

In our seasonal movement model, including the lek-to-mesic resource layer as an additional conservation feature resulted in the selection of areas located around larger leks, closer to mesic

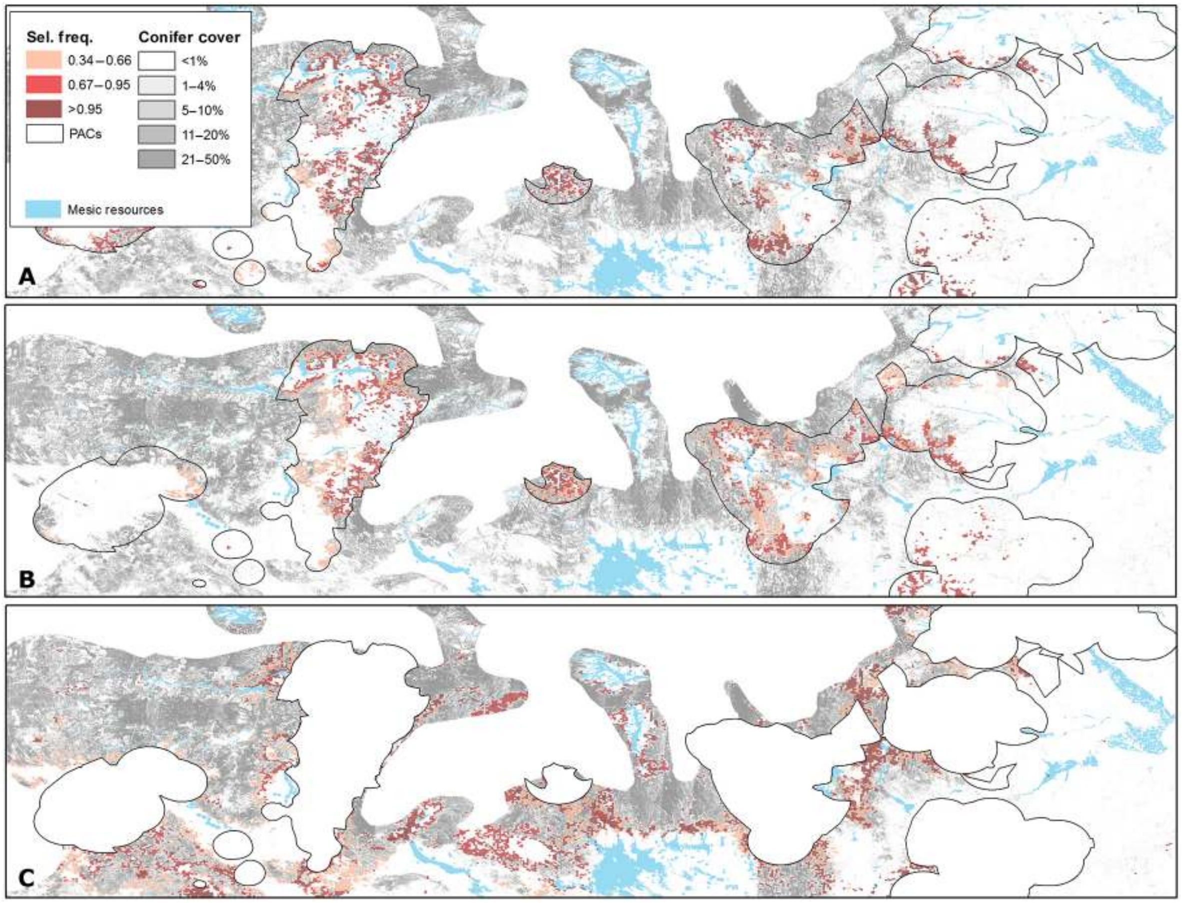

Fig. 4. Maps illustrating the distribution of medium and higher importance (selection frequency >0.33) conifer removal areas across a portion of eastern Oregon for (A) breeding habitat enhancement, (B) seasonal movement, and (C) between-priority areas of conservation connectivity optimization models.

resources, and within potential pathways which if cleared of expanding conifer could connect bird movements from breeding to late brood-rearing habitats (Fig. 5). Similar to the breeding habitat enhancement model, grid cells with lower tree canopy cover and higher R&R values were selected more often, and as anticipated, accounting for seasonal bird movement to mesic habitats resulted in more hexagons being placed into high sf categories (Fig. 2). Increased mortality risk may be associated with longer travel between seasonal habitats, and based on new research (Gibson et al. 2016), we hypothesize that high sf hexes may represent a threshold distance between seasonal habitats wherein female nest site selection is as much a reflection of chick survival as it is nest success. This biology is reflected in selection frequencies wherein hexagons with high lek-to-mesic movement values and the lowest cost factor (e.g., lower canopy cover and higher R&R; see *Methods*) are chosen with high frequency (i.e., sf > 0.7), while higher cost hexagons are chosen less frequently (i.e., sf < 0.6; Appendix S1: Fig. S1). The uptick in 0.25–0.5 selection frequencies relative to the breeding habitat enhancement model likely reflects isolated mesic resources that support small breeding populations where conifer removal would result in fewer benefits to populations (Donnelly et al. 2016). Improving movement capability to reach late brood-rearing habitats, and decreasing the risk associated with these movements have emerged as conservation priorities (e.g., Dahlgren et al. 2016) as the cost to

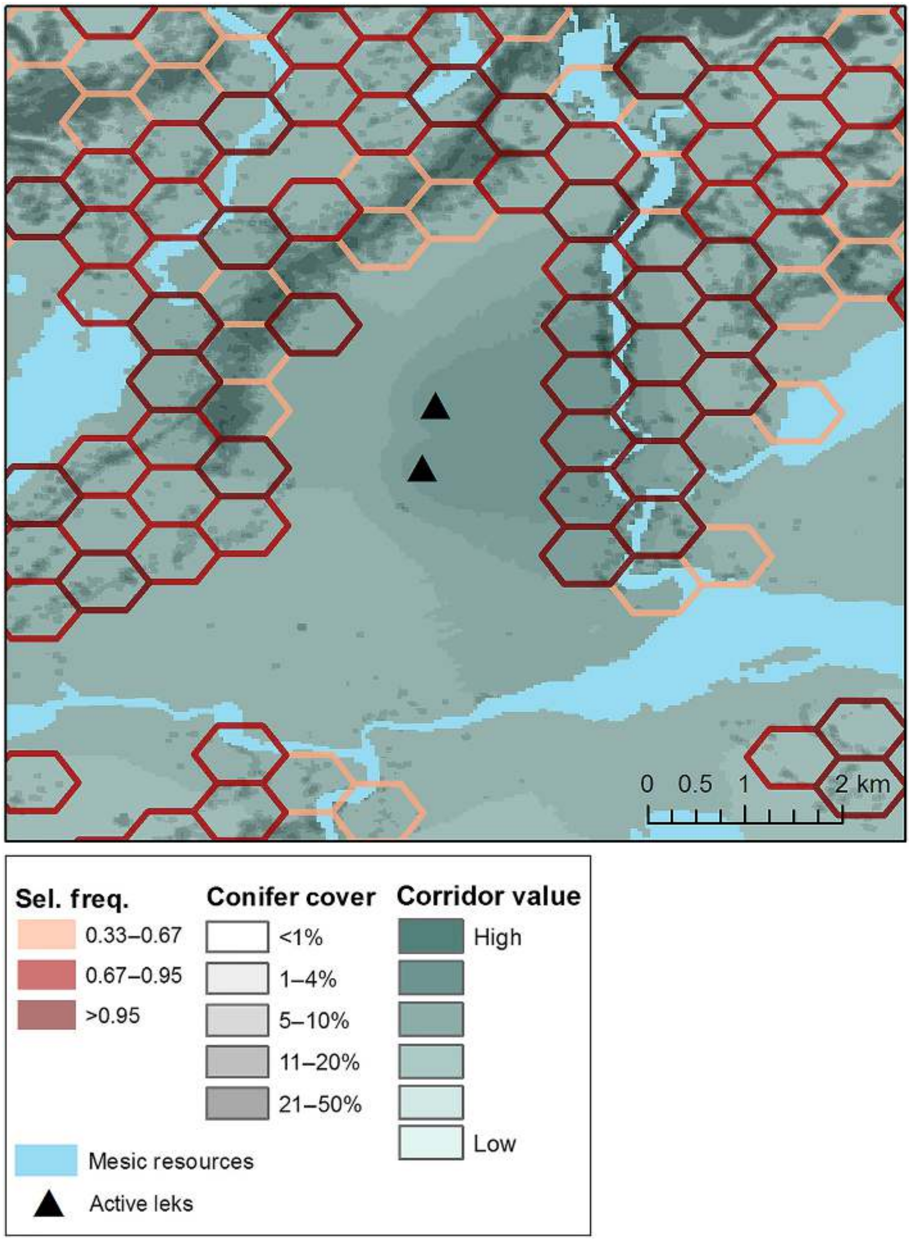

Fig. 5. An example of potential conifer removal areas as predicted by the seasonal movement model. The relative importance of each grid cell is indicated by selection frequency, in red. The inclusion of other ecosystem characteristics, beyond just lek locations, provides the ability to prioritize conifer removal and better maximize the biological return on investment.

sage-grouse of navigating conifer woodlands is better understood (Prochazka et al. 2017).

Our between-PAC connectivity model preferentially selected removal along pathways of high sage-grouse movement potential (as calculated by Knick et al. 2013) and around leks located outside of PACs (Fig. 6). Areas with lower conifer cover were selected more often, but high canopy cover areas were also selected to a lesser extent, generally in areas with high movement potential (Fig. 6). Maintenance of habitat quality along movement pathways is vital as these areas

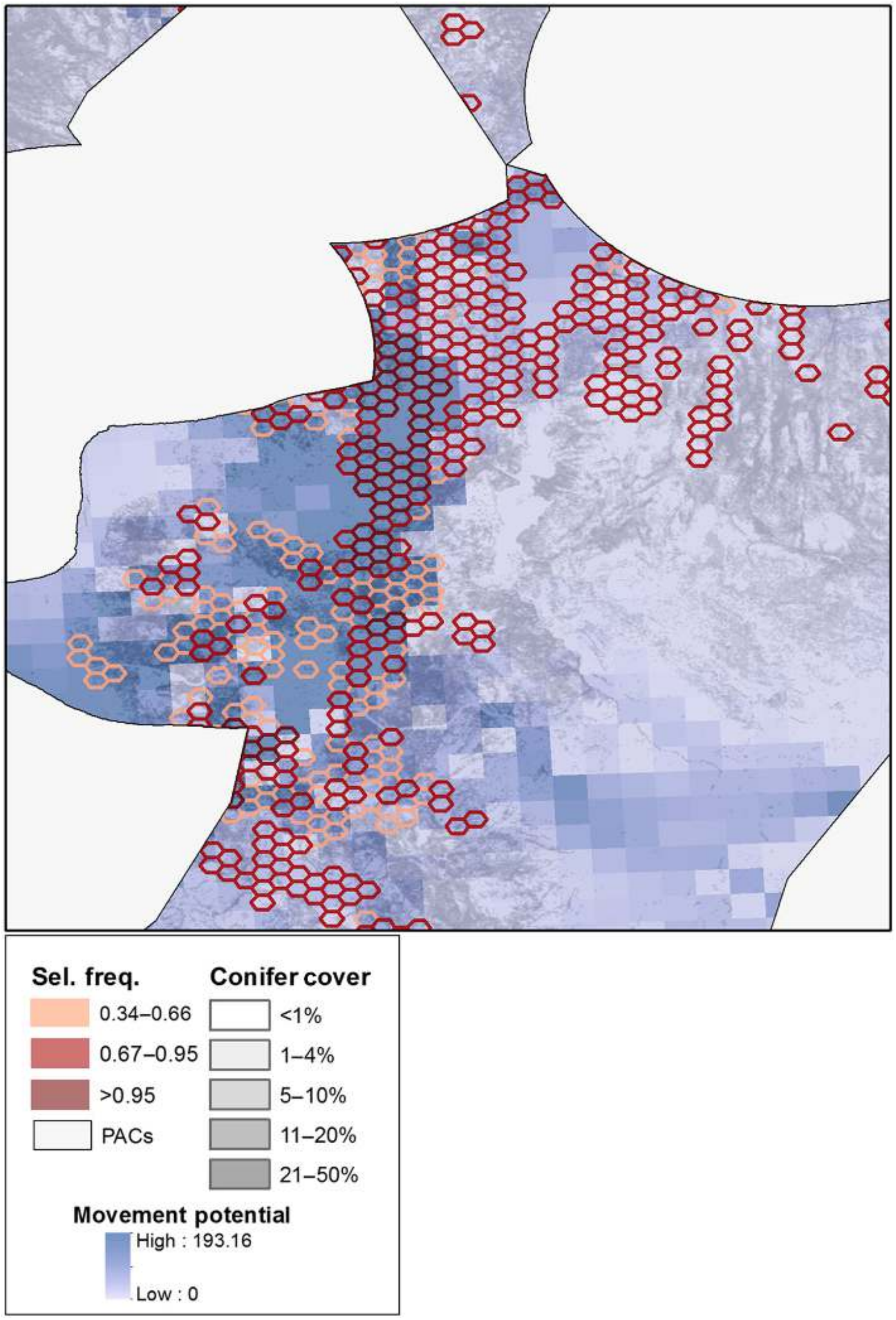

Fig. 6. An example of potential conifer removal areas as predicted by the between-priority areas of conservation (PAC) connectivity model. The relative importance of each grid cell is indicated by selection frequency, in red.

serve as stopover and refueling areas (Newton et al. 2017). The skewed distribution of hexagon sf in the between-PAC connectivity model (Fig. 2) likely is a reflection of the large land area between PACs (4.9 million ha) than within them (2.6 million). Current sage-grouse management prioritizes within-PAC conservation (USFWS 2013), and limited resources make it hard to justify between-PAC conifer removal until habitats supporting population strongholds are restored.

Nevertheless, connectivity (Wiens 1995, McCullough 1996, Hanski 1998, Crist et al. 2017) and genetic diversity (Shirk et al. 2015) are important too, and perhaps someday our between-PAC model (Fig. 6) could be used to select a landscape in which to test the efficacy of conifer removal in restoring connectivity among population centers or PACs.

Most lands where conifer removal would benefit grouse connectivity are federally managed by BLM and to a lesser extent USFS (United States Forest Service) and USFWS, as indicated by a plurality of medium- and higher-priority hexagons (sf > 0.33) highlighted by our between-PAC connectivity model (Table 2). In contrast, the prevalence of private lands identified for management by our seasonal movement model (Table 2) corresponds with recent work by Donnelly et al. (2016) whose regional mapping shows that 80% of mesic resources reside on well-watered and productive private lands used primarily for cattle ranching. These land ownership dynamics further highlight the importance of public/private partnerships in the context of sage-grouse conservation. Strategies that combine management efforts across ownerships will likely be needed to achieve desired landscape-scale outcomes in conservation.

We also compared our results to one case study of landscape-scale conifer removal occurring across public and private lands to evaluate model performance in an applied context (Fig. 7). The bulk of the conifer removal efforts in the Warner Mountains region have been conducted south of Oregon highway 140 (Fig. 7), primarily on public land (U.S. BLM). North of the highway, conifer removal efforts have not yet been completed on public lands—the only cuts north of the highway have been conducted on private land, primarily on the western end of the study area (Fig. 7). Overall, the proportion of overlap between more optimal conifer removal areas (sf > 0.33) as predicted by our models and treatment areas in the Warner Mountains exhibits a general decrease over time (Fig. 3). This suggests that managers in the project area may have treated the most optimal areas early on, and subsequently cut conifer in less optimal areas as time progressed. Our results also suggest that there is an abundance of potentially important conifer removal areas (s.f. > 0.33) north of highway 140, where removal efforts

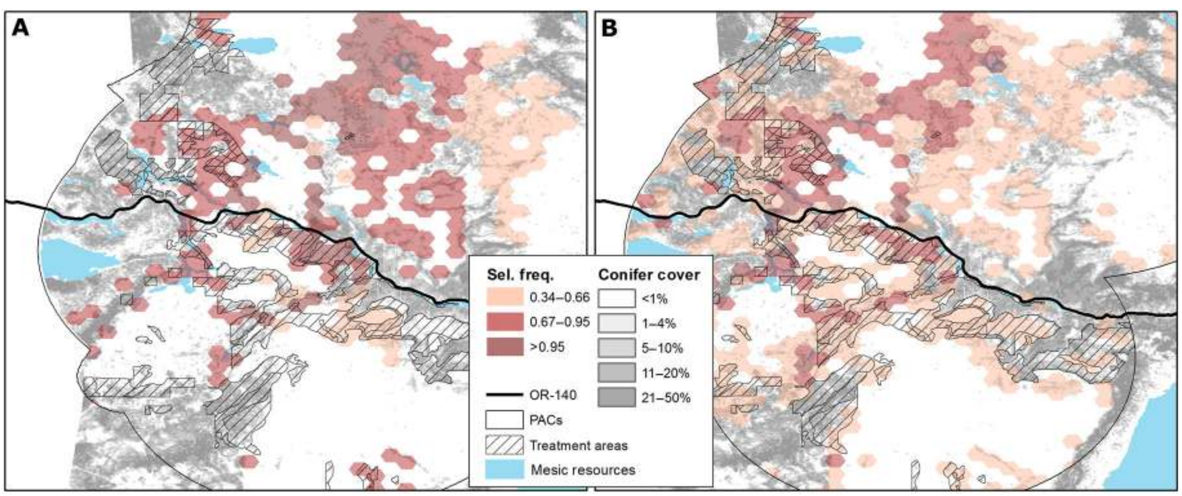

Fig. 7. A comparison of recent Warner Mountain conifer treatment areas and model output for the (A) breeding habitat enhancement and (B) seasonal movement optimization models. Models were constructed based on pre-treatment conditions. The relative importance of each grid cell is indicated by selection frequency, in red. The optimization framework largely corresponds with current, on-the-ground removal efforts. The bulk of conifer treatment areas are located south of Oregon highway 140 (thick black line). Mapped treatments conducted north of highway 140 are located on private lands; efforts on public lands north of highway 140 are still in an early or planning stage. PACs, priority areas for conservation.

have yet to be conducted on public lands. These results may be a useful addition to the planning toolbox for management efforts in the area, especially for considering both breeding and brooding habitat for sage-grouse.

Outcome-based evaluations in the Warner Mountains show that within three years of management, one-third of radio-marked sage-grouse shifted their nesting to conifer cuts; no such behavioral change occurred in the non-cut control areas where conifer expansion continues (Severson et al. 2017*a*). Moreover, sagebrush-obligate songbird abundance doubled post-treatment (Holmes et al. 2017), suggesting that cooperative removal strategies on BLM and private lands extend to obligate species other than grouse. While much of the conifer removal in the Warner Mountains was primarily intended to benefit grouse, the whole landscape approach to restoration also included other species goals, such as habitat improvements for big game including mule deer and bighorn sheep; concomitant benefits to these species are yet to be fully assessed.

Multi-objective systematic landscape optimization models (such as Marxan) have been in use for over a decade to inform reserve planning (Game et al. 2008, Ball et al. 2009, Watts et al. 2009, Schneider et al. 2012, Bino et al. 2015, Braid and Nielsen 2015), strategically manage invasive species (Januchowski-Hartley et al. 2011), and optimize conservation of ecosystem services (Chan et al. 2011, Egoh et al. 2011, Schroter and Remme 2016). Most recently, Farzan et al. (2015) used landscape optimization models in sagebrush ecosystems to optimize juniper management for sage-grouse breeding habitat and cattle forage production. Here, we extend the utility and demonstrate flexibility of optimization modeling to incorporate new spatial information across multiple scales, including the distribution of late brood-rearing habitat, landscape-level connectivity, proactive federal lands restoration, and local management objectives. Much of this information was agreed upon in a scoping process that included stakeholders (e.g., SGI, NRCS). In addition to producing actionable coproduced science, the optimization framework demonstrated here can also allow managers to better estimate the financial investments necessary to achieve desired biological returns on investment. For example, using simple estimates of \$30/acre for 1–4% conifer cover, \$150/ac for 5–10% cover, and \$200/ac for 11–20% cover, it would cost ~\$1 million USD to treat the most important areas (sf > 0.95) within PACs based on the seasonal movement model, or a \$10 million USD investment to enhance the broader landscape (sf > 0.66).

Although the models presented here produce a series of spatially explicit optimizations for targeting conifer removal efforts, it is the conceptual framework behind the models that we emphasize. In constructing optimization models for this study, we assumed that lek population data and breeding habitat models adequately represented breeding habitat quality, and we did not include assessments of other landscape fragmentation, such as wildfire or development risk. We also acknowledge the very real difference between heuristic estimates of connectivity (i.e., Circuitscape) and on-the-ground functional connectivity as realized by sage-grouse populations. Within this framework, we focused exclusively on sage-grouse conservation goals, but recognize that non-target species impacts are one of the potential pitfalls of planning management efforts around a single focal species. One of the advantages of using a systematic approach to landscape optimization, however, is adaptability. Additional factors or competing interests can be incorporated with relatively little additional effort (Ball et al. 2009). For example, others may seek to balance woodland- and sagebrush-obligate species needs, or plan comprehensive watershed treatments that optimize specific treatment techniques (e.g., mechanical cutting vs. prescribed fire) to achieve a mosaic of conditions across the landscape through time and space (Boyd et al. 2017). Such adaptability—in optimization, planning, and implementation—is necessary for conservation to be successful (Hiers et al. 2016).

Conclusions

Enhancing and expanding sage-grouse habitat by removing encroaching conifers has become one of the few options available for achieving uplift in sage-grouse habitats in a relatively short time period (Miller et al. 2017). Planning and implementing large-scale management efforts is time-consuming and expensive; with limited resources, it is critical that biological return on investment be maximized to the extent possible. In the sagebrush ecosystem in particular, this task has proven especially difficult due to the lack of landscape assessment tools. However, recent advances have been made through development of detailed datasets including conifer cover (Falkowski et al. 2017), mesic resources (Donnelly et al. 2016), breeding habitat suitability (Doherty et al. 2016), and connectivity (Knick et al. 2013). We built upon this recent work to test three landscape-level optimization models to target conifer removal in habitats across the sage-grouse life cycle (breeding and brood rearing), and to improve between-PAC connectivity and gene flow. The optimization framework and models applied in this study are designed to illustrate analyses increasingly accessible to land managers that can augment, but not replace, expert-based approaches to planning and prioritization.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1888/full