A conservation planning tool for Greater Sage-grouse using indices of species distribution, resilience, and resistance

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Abstract. Managers require quantitative yet tractable tools that identify areas for restoration yielding effective benefits for targeted wildlife species and the ecosystems they inhabit. As a contemporary example of high national significance for conservation, the persistence of Greater Sage-grouse (*Centrocercus urophasianus*) in the Great Basin is compromised by strongly interacting stressors of conifer expansion, annual grass invasion, and more frequent wildfires occurring in sagebrush ecosystems. Associated restoration treatments to a sagebrush-dominated state are often costly and may yield relatively little ecological benefit to sage-grouse if implemented without estimating how Sage-grouse may respond to treatments, or do not consider underlying processes influencing sagebrush ecosystem resilience to disturbance and resistance to invasive species. Here, we describe example applications of a spatially explicit conservation planning tool (CPT) to inform prioritization of: (1) removal of conifers (i.e., pinyon-juniper); and (2) wildfire restoration aimed at improving habitat conditions for the Bi-State Distinct Population Segment of Sage-grouse along the California–Nevada state line. The CPT measures ecological benefits to sage-grouse for a given management action through a composite index comprised of resource selection functions and estimates of abundance and space use. For pinyon-juniper removal, we simulated changes in land-cover composition following the removal of sparse trees with intact understories, and ranked treatments on the basis of changes in ecological benefits per dollar-unit of cost. For wildfire restoration, we formulated a conditional model to simulate scenarios for land cover changes (e.g., sagebrush to annual grass) given estimated fire severity and underlying ecosystem processes influencing resilience to disturbance and resistance to invasion by annual grasses. For both applications, we compared CPT rankings to land cover changes along with sagebrush resistance and resilience metrics. Model results demonstrated how the CPT can be an important step in identifying management projects that yield the highest quantifiable benefit to Sage-grouse while avoiding costly misallocation of resources, and highlight the importance of considering changes in sage-grouse ecological response and factors influencing sagebrush ecosystem resilience to disturbance and resistance to invasion. This unique framework can be adopted to help inform other management questions aimed at improving habitat for other species across sagebrush and other ecosystems.

Key words: cheatgrass; Great Basin; invasive species; resilience; resistance; restoration; sagebrush; Sage-grouse; species distribution model; wildfire.

Introduction

Managers responsible for the recovery of species or for mitigating impacts of anthropogenic development and ecological disturbance need tractable tools to maximize ecological benefits per unit of economic costs (Noss et al. 1997). Modeling capacity to address this need has been strengthened by the proliferation of species distribution models (SDM) that are spatially explicit. These powerful models typically use input from presence-pseudoabsence survey data or individually based telemetry location data that inform statistical functions within geographic information systems (GIS) to create predictive surfaces describing the relative probabilities of occurrence and resource use across multiple spatiotemporal scales (Guisan and Zimmermann 2000, Rushton et al. 2004, Johnson and Gillingham 2005, Guisan et al. 2013). While the number of studies describing methods for SDMs and recognition of their benefits for conservation planning has increased drastically in the last decade (Guisan et al. 2013), few examples exist in the peer-reviewed literature describing the real-world application of these models to actual conservation decision-making. As a result, there is a call for "more practice orientated assessments" (Guisan et al. 2013) of these models and greater collaboration among managers (those responsible for decision-making) and researchers (those responsible for delivering usable information) during the subsequent development and implementation of conservation planning. The applicability

of these models to inform effective management action is often dependent on spatial scale, ecological context (Stephens et al. 2015), and the types of population response indices incorporated (Coates et al. 2016a).

Species distribution models based on restrictive scales and single indices are not a panacea for conservation problems for at least two reasons. First, applying predictive models derived from local studies across broader regional scale models may not yield effective conservation solutions if animal abundance and distribution are not considered (Pulliam 2000, Guisan et al. 2006). Results from "spatially invariant" models (Guisan et al. 2006) that only consider effects on habitat suitability lead to ineffective restoration if model output supports treatment implementation in areas where habitat suitability would be improved but the chances of actual use by the species of concern is low because source populations are too distant. In such cases, broad-scale population data can facilitate the development of integrative methods to create composite spatially explicit indices that reflect actual abundance and habitat information (Coates et al. 2016a, Doherty et al. 2016, Reinhardt et al. 2017).

Second, the underlying processes controlling ecosystem resilience and resistance can influence effectiveness of management action. Resilience is a measure of the capacity of ecosystems to reorganize and regain their fundamental structure, processes, and function following stressors (e.g., drought) or disturbances (e.g., fire; Holling 1973, Standish et al. 2014). Resistance is a measure of the capacity of ecosystems to remain largely unchanged and retain their fundamental structure, processes, and function despite exposure to stressors such as disturbances or invasive species (Folke et al. 2004). SDMs alone do not inherently incorporate these concepts, which can lead to costly misallocation of limited funding towards ineffective restoration efforts in areas that have a low likelihood of recovery following a disturbance compared to areas of high resilience where recovery from passive or active restoration is likely more effective (Chambers et al. 2014a).

Greater Sage-grouse (*Centrocercus urophasianus;* hereafter Sage-grouse) require large continuous areas of sagebrush for population persistence (Knick et al. 2013) and are considered an umbrella species for the conservation of sagebrush ecosystems at landscape scales (Rowland et al. 2006). Sage-grouse have been considered frequently for listing under the Endangered Species Act (ESA; U.S. Fish and Wildlife Service 2015a) as their populations have declined concomitantly with the loss and fragmentation of sagebrush ecosystems across western North America (Schroeder et al. 2004, Miller et al. 2011). In the western portion of the species range, population declines have been associated with a number of well-documented stressors to sagebrush ecosystems that include, but are not limited to, conifer expansion, invasive annual grasses, and altered wildfire regimes (U.S. Fish and Wildlife Service 2015a). These stressors can strongly alter ecosystem attributes and processes that previously allowed sagebrush ecosystems to recover after disturbance (Chambers et al. 2014a, Miller et al. 2014). An ecological threshold may be crossed once ecosystem processes have been modified beyond the limits of ecological resilience, and the ecosystem may switch to a degraded state that is unrecoverable without intensive management intervention (Westoby et al. 1989, Standish et al.

2014). For example, changes in land use practices, wildfire suppression, and altered climate over the last 150 yr have increased the likelihood of expansion and infill of singleleaf pinyon (*Pinus monophylla*) and Utah juniper (*Juniperus osteosperma*; hereafter pinyon–juniper) into sagebrush ecosystems once devoid of trees (Miller et al. 2005, 2008, 2011, Romme et al. 2009, Baruch-Mordo et al. 2013). Dominance of sagebrush and perennial grasses, which contribute strongly to sagebrush ecosystem resilience to disturbance and resistance to invasion (hereafter RR; Chambers et al. 2014a), declines concomitantly as pinyon–juniper canopy increases (Miller et al. 2005). Moreover, higher loadings of coarse woody fuels resulting from pinyon–juniper expansion can lead to more severe wildfires that also burn underlying or adjacent fire-intolerant sagebrush (Strand et al. 2013). Following these high severity wildfires, invasive annual grasses that primarily include cheatgrass (*Bromus tectorum*) can form homogeneous and competitively dominant stands (Miller et al. 2005, 2011, Condon et al. 2011), especially at lower elevations with warmer and drier climates. The subsequent increase in the amount and continuity of fine fuels from invading annual grass can increase the frequency of large wildfires that spread to adjacent stands of intact sagebrush that would otherwise burn less frequently (D'Antonio and Vitousek 1992, Brooks et al. 2004, Chambers et al. 2007, 2014a, Balch et al. 2013). Accordingly, sagebrush management practices and policy are focused increasingly on identifying factors influencing RR, and integrating these concepts with larger-scale ecological minima for Sage-grouse to guide decisions for restoration (Chambers et al. 2014c).

The degradation and loss of sagebrush through the expansion of pinyon–juniper and altered wildfire-annual grass cycles diminishes habitat value to Sage-grouse and other sagebrush dependent wildlife species through many mechanisms. For example, trees provide elevated perch and nesting substrates in an otherwise two-dimensional landscape for avian predators such as raptors and Common Ravens (*Corvus corax*; Howe et al. 2014) that can negatively influence Sage-grouse behavior and demography (Coates and Delehanty 2008, 2010). Even a small amount of pinyon–juniper expansion (e.g., <2% cover) can decrease the probability of Sage-grouse using otherwise suitable habitat (Doherty et al. 2008, Atamian et al. 2010, Casazza et al. 2011, Baruch-Mordo et al. 2013, Knick et al. 2013, Severson et al. 2017). Moreover, encountering pinyon–juniper can lead to more risk-prone behavior by Sage-grouse (Prochazka et al. 2017), and selection of highly productive sagebrush habitat with scattered trees has negative fitness consequences for Sage-grouse (Coates et al. 2017b). Invasion by annual grasses also diminishes habitat suitability by reducing available nesting cover and forage (Crawford et al. 2004, Kirol et al. 2012, Lockyer et al. 2015), which can contribute to depressed population growth (Blomberg et al. 2012).

Patterns of Sage-grouse abundance and space use often align closely with the distribution of Sage-grouse leks (Doherty et al. 2011, Fedy et al. 2012, Coates et al. 2013). Thus, the distribution of leks in relation to landscape characteristics can be used in SDMs for Sage-grouse at large spatial scales (e.g., Baruch-Mordo et al. 2013, Knick et al. 2013). Other Sage-grouse SDMs have relied on more traditional approaches utilizing locations of radio-marked Sage-grouse

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in relation to available habitat across seasons within relatively small study sites (e.g., Doherty et al. 2008, Atamian et al. 2010, Aldridge et al. 2012, Dzialak et al. 2012). Investigators working at regional and rangewide spatial scales have begun combining output from SDMs quantifying Sage-grouse resource selection derived from either lek absence–pseudoabsence survey data (Doherty et al. 2016, Reinhardt et al. 2017) or extensive radio-telemetry location data (e.g., Coates et al. 2016a) with output from SDMs quantifying Sage-grouse abundance and distribution based on lek counts. When properly calibrated and validated (Stephens et al. 2015), indexed output from these approaches can yield a proxy for complex ecological processes that include resource selection, distribution, and abundance at multiple spatial scales. Composite indices can also help guide more effective targeting of management actions because they are less prone to shortcomings of singular SDMs that only take one index (e.g., resource selection, distribution, or abundance) into account at a time. Accordingly, a composite index modeled with real-world data can provide the currency for a real-world management decision support tool. Such a tool could identify areas with high index values that describe habitat features selected strongly by Sage-grouse in areas within close proximity to existing Sage-grouse populations based on lek distribution and attendance. Given this information, changes in land cover following management actions (e.g., conifer removal and wildfire restoration) can be simulated in a GIS framework and composite index values recalculated. When evaluated with spatially explicit information on ecosystem attributes that predict how a potential restoration site can withstand disturbance and resist invasion, managers would be armed with a tool that helps strategically direct management actions in areas that optimize ecological benefits to Sage-grouse populations and sagebrush ecosystems.

Sage-grouse that occur along the border of California and central Nevada represent the extreme southwestern extent of the species' range (Schroeder et al. 2004) and are referred to as the "Bi-State" population. Compared to the remainder of the species' range, the Bi-State population is spatially isolated (Schroeder et al. 2004), genetically distinct (Benedict et al. 2003, Oyler-McCance et al. 2015), and can use different habitat components to meet life history needs (Kolada et al. 2009a, b, Casazza et al. 2011). Some Bi-State sub-populations have also displayed declining trends in lek attendance (Coates et al. 2018). These factors, in part, prompted the U.S. Fish and Wildlife Service to identify Sage-grouse in the Bi-State as a distinct population segment (DPS; U.S. Fish and Wildlife Service 2010) and propose it for listing as threatened under the ESA in December 2013 (U.S. Fish and Wildlife Service 2013). However, the proposed listing was withdrawn in April 2015 (U.S. Fish and Wildlife Service 2015b), which was due in part to the creation of an adaptive management plan developed by a team of state and federal research biologists, agency managers, and stakeholders (Bi-State-Action-Plan 2012).

Rich data sets describing the Bi-State DPS are available for developing a Conservation Planning Tool (CPT) that integrates population and scaled habitat data to identify areas for potential management action that could better maximize ecological benefits to Sage-grouse and the sagebrush ecosystems that they depend upon. Here, we describe the development of a CPT for Sage-grouse based on the product of two empirically derived indices: (1) resource selection functions (RSF, a type of SDM) and (2) composite abundance and space-use indices (AUI, a type of SDM based on the distribution of Sage-grouse leks and male attendance). We then provide two example applications for how the CPT can inform spatially explicit prioritization of two adaptive management actions with interrelated ecological processes: (1) removal of low-density pinyon–juniper expanding into sagebrush and (2) post-wildfire sagebrush ecosystem restoration. In these examples, we also demonstrate how CPT metrics focused on restoration impacts to Sage-grouse ecology can be used for comparison or be integrated with sagebrush ecosystem metrics that focus on RR. The conceptual framework underlying the CPT that we present here can be applied readily to other situations where there is a desire to use empirical data on species space use and resource selection to prioritize management actions intended to improve conditions for species of conservation concern.

Methods

Study area

The Bi-State area comprises 18,325 km^2 spanning the border of Nevada and California at the interface of the Sierra Nevada Mountains to the west and the Great Basin to the east (Fig. 1). Elevation ranges from 1,386 m to 4,344 m, with rugged mountains separated by broad valleys. Floristically, sagebrush habitats are similar to those found in the Great Basin, and dominated by Wyoming big (*Artemesia tridentata wyomingensis*), mountain big (*A. tridentata vaseyana*), black (*A. nova*), and low (*A. arbuscula*) sagebrush species. Other native common shrubs include rabbitbrush (*Chrysothamnus* spp.) and antelope bitterbrush (*Purshia tridentata*). Native perennial grasses include Great Basin wildrye (*Leymus cinereus*), needle grass (*Achnatherum* spp.), ricegrass (*Achnatherum hymenoides*), and squirreltail (*Elymus elymoides*), while cheatgrass (*Bromus tectorum*) is the most common nonnative annual grass.

Sage-grouse telemetry

We used location data ($n = 15,247$) from 290 radio-marked Sage-grouse captured at six sites across the Bi-State from 2003 to 2013. Sites, from north to south, were Pine Nuts, Desert Creek, Mt. Grant, Bodie Hills, South Mono, and Long Valley (Fig. 1). For RSF modeling, locations from Desert Creek, Bodie Hills, and Mt. Grant were pooled, an approach supported by low genetic divergence among these sub-populations (Oyler-McCance et al. 2015). All Sage-grouse were captured at night using spotlighting techniques (Wakkinen et al. 1992), sexed according to plumage and morphological characteristics (Dalke et al. 1963), and fitted with a 21-g necklace-style very high frequency (VHF) radio-transmitter (Advanced Telemetry Systems, Isanti, Minnesota, USA). Females comprised the majority (70–84%) of marked individuals within sites. A subset of Sage-grouse ($n = 30$) from Bodie Hills and Pine Nuts were also fitted with a rump-mounted and Teflon-tape secured Global Positioning System—Platform Transmitter Terminal (GPS-PTT; Northstar Science and Technology, King George, Virginia,
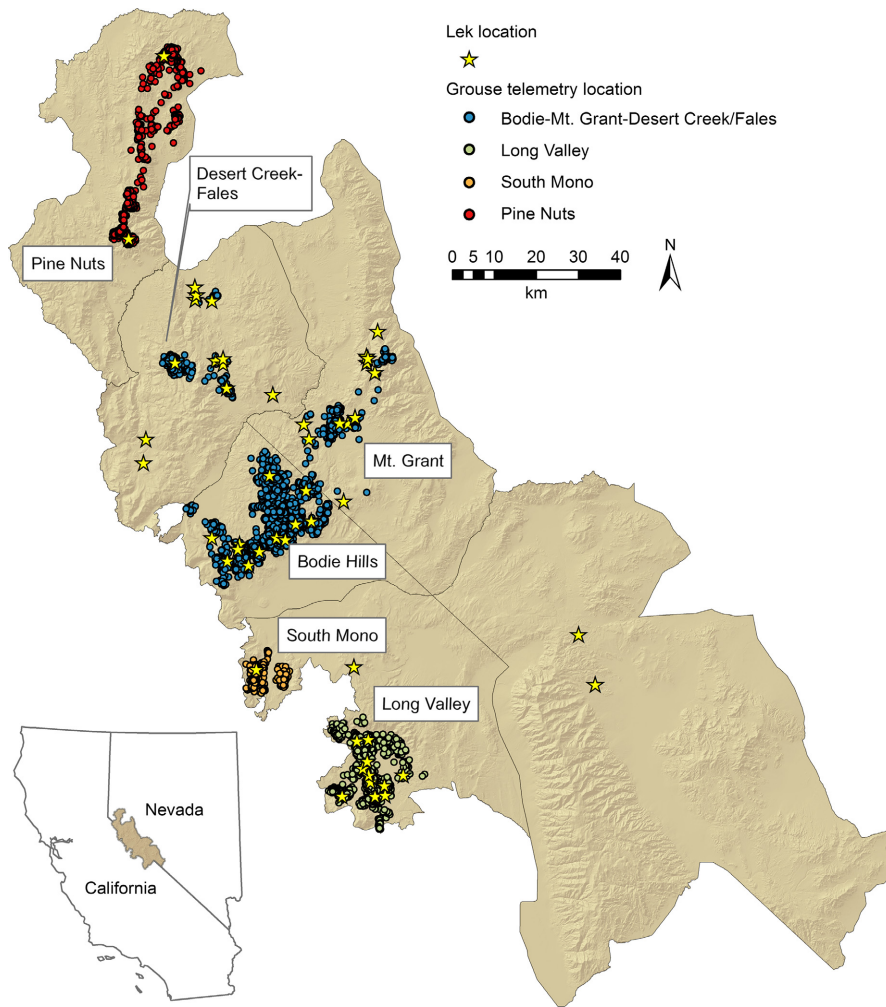
Fig. 1.   Locations of radio-marked Greater Sage-grouse by study site used for resource selection modeling and locations of leks used to derive the abundance and space use index within the Bi-State Distinct Population Segment.

USA). These units were also fitted with a small (<1.0 g) VHF transmitter to help expedite ground location of any mortalities, but were not used to systematically locate live birds. Hence, location data sets for individual birds were either VHF-only or GPS-PTT derived. Maximum mass of VHF-only transmitters or GPS-PTT units did not exceed 3% of Sage-grouse body mass. We used handheld radio-receivers and Yagi antennas to circle locations of VHF-marked Sage-grouse within approximately 30 m, and were careful to avoiding flushing birds. The majority of VHF locations across sites (79–98%) were obtained during the spring and summer months when Sage-grouse were typically located more than two times per week. Universal Transverse Mercator (UTM) coordinates were recorded with a hand-held GPS unit. Sage-grouse fitted with GPS-PTT units yielded up to 12 locations per day during crepuscular and diurnal hours, but we used only one randomly selected location per day for analyses to maintain compatibility among VHF and GPS-PTT data sets and minimize serial autocorrelation. We further restricted the data set for both types of units to only include Sage-grouse with three or more relocations in which grouse were confirmed to be alive.

GIS based landscape features

Owing to the lack of a singular land cover classification spanning our study area, we used multiple Landsat-derived mapping products to classify generalized land cover types at a 900-m² resolution (Appendix S1; Appendix S2: Fig. S1). Except for annual grass, only those land cover types comprising >2% of the study area were used in our analyses to minimize the influence of rarity and simplify the number of variable combinations used in model selection (see *RSF modeling*). Land cover types >2% included low sagebrush, Wyoming big sagebrush, mountain big sagebrush, lowland non-sagebrush shrub (hereafter lowland shrub), and riparian. Annual grass cover type, including cheatgrass, comprised slightly less than 2% of the study area but was included in analyses due it is importance for the post-wildfire restoration example.

Pinyon–juniper was abundant throughout the study area as determined from the Landsat-derived products, but we did not explicitly include this layer in our predictive analysis because the spatial resolution proved too coarse to identify the early stages of pinyon–juniper expansion that can strongly

influence Sage-grouse behavior and demographic performance (Baruch-Mordo et al. 2013, Coates et al. 2017*b*, Prochazka et al. 2017, Severson et al. 2017). Rather, we mapped cover of pinyon–juniper at a finer 1-m^2 resolution using 2013 National Agriculture Imagery Program (NAIP) imagery, whereby circular canopy extent and spectral signature from four-band color-infrared images were classified with object recognition algorithms in Feature Analyst (Overwatch Systems, Sterling, Virginia, USA) as described in more detail by Coates et al. (2017*a*). Although our mapping process could not readily distinguish among conifer species, we refer to all mapped conifers as pinyon–juniper because they dominated composition of conifers in our study area. This mapping process has also formed the basis for recent high-resolution studies of Sage-grouse behavioral and demographic responses to encountering pinyon–juniper at different densities (Coates et al. 2017*b*, Prochazka et al. 2017).

A series of steps were then taken to modify the base pinyon–juniper map for the following reasons. First, pinyon–juniper mapped at 1 m^2 needed to be rescaled to a resolution that would be comparable with Landsat-derived land cover types, yet still allow identification of scattered trees. Second, we needed to identify Landsat-derived land cover that intersected pinyon–juniper below a specified threshold of tree cover because (1) resource selection response by Sage-grouse likely differed when scattered or co-dominant pinyon–juniper did or did not co-occur with intact herbaceous and shrubland understories (Coates et al. 2017*b*) and (2) our pinyon–juniper removal example required identification of land cover (particularly herbaceous and shrubland types) that could be restored immediately following the removal of low density trees. Accordingly, we first derived a map representing a continuous percentage of pinyon–juniper cover at the 1-m^2 resolution using a circular moving window with a 100-m radius (ArcGIS Spatial Analyst, Environmental Systems Research Institute, Redlands, California, USA), and then resampled it to a Landsat-comparable 900-m^2 resolution. We also created a simple "raw pinyon–juniper" map, whereby any 900-m^2 pixel intersecting any pinyon–juniper value was set to a value of one at the 1-m^2 scale. This binary process alone would over represent tree cover, so we used raw pinyon–juniper as a covariate for describing pinyon–juniper cover in conjunction with the three classes of categorized pinyon–juniper cover derived from the continuous percentage map. Following Falkowski et al. (2017), the categorized cover classes were intended to correspond broadly to phases of conifer expansion into sagebrush as described by Miller et al. (2005) and illustrated in Appendix S2: Fig. S2. Cover-class 1 represented 0.01–10% tree canopy cover and approximated Phase 1 expansion where shrubs remain dominant over pinyon–juniper. Cover-class 2 represented 10–20% cover and approximated Phase 2 where shrubs and pinyon–juniper co-dominate. Cover-class 3 represented >20% cover and approximated Phase 3 with sparse understory and dominant pinyon–juniper. Canopy cover was calculated at the original 1-m^2 scale and then up-scaled to 900 m^2 using nearest neighbor resampling in Spatial Analyst. We then reclassified all Landsat-derived land cover types intersecting the categorized pinyon–juniper map with <20% canopy cover as pinyon–juniper understory (hereafter "understory"), which corresponded to assumed ground conditions where shrubs and

herbaceous vegetation remain at least co-dominant (e.g., ≤Phase 2). Pixels with >20% cover were classified as only pinyon–juniper with no understory. Pixels erroneously classified by Landsat imagery as pinyon–juniper relative to comparisons with the cover-class map were reclassified based on the dominant surrounding land cover type within 1 km.

Because variation in resource selection and avoidance is influenced strongly by how Sage-grouse perceive a landscape spatially (Doherty et al. 2008, Casazza et al. 2011, Aldridge et al. 2012), we measured resources available to Sage-grouse at ecologically relevant spatial scales. For land cover, we measured the proportion of each land cover type in each 900-m^2 pixel using circular moving windows with areas of 9 ha, 61 ha, and 661 ha calculated with radii that represented the minimum (167.9± 0.6 m [mean ± SE]), mean (439.5 ± 0.6 m), and maximum (1,451.7 ± 1.7 m) daily distance traveled across all radio-marked Sage-grouse in this study. We calculated these descriptive statistics by calculating the distance traveled between each successive location divided by the number of elapsed days between locations for each grouse, and then took the average of the minimum, mean, and maximum of these movements. Location data for GPS-PTT marked grouse data were rarified by randomly selecting one point per day per grouse, and no VHF marked grouse had more than one location per day.

We also measured two groups of predictor variables to describe proximity to water source and topographic variation effects on Sage-grouse resource selection. Water source features in the candidate set included perennial streams, intermittent streams, all streams, springs, and open water bodies (Appendix S1). Linear relationships were assessed as the Euclidean distance to a water source from a point, while non-linear relationships were assessed with an exponential decay function, $e^{-d/\alpha}$ (Nielsen et al. 2009), where d was the linear distance to feature (used or random point), and α was the mean linear distance from used points to that feature. Topographic variables in the candidate set included elevation, topographic position index, and surface roughness (Appendix S1).

Recent research has demonstrated how variation in underlying soil temperature and moisture regimes govern resilience to disturbance and resistance to annual grass invasion in sagebrush ecosystems, where, in general, higher elevation sites dominated by soils with cool or cold temperature and wetter moisture regimes have higher RR than lower elevation sites with warmer and drier soils (Chambers et al. 2014*a, b*). We extracted generalized RR index values (high, moderate, and low) within our study area from a map developed by Maestas et al. (2016) (map *available online*[9]; Appendix S2: Fig. S3) for either post-hoc comparison (pinyon–juniper removal example) or direct integration (post-wildfire restoration example) with CPT outputs.

RSF modeling.—While our overall CPT framework is not confined to using just one specific type of SDM to model resource selection, we chose to use RSFs that are very well suited and widely used to model data generated from wildlife telemetry studies. RSFs estimate selection and avoidance for particular landscape features by contrasting measurements

[9] https://map.sagegrouseinitiative.com/

at used locations (telemetry points) with measurements at random locations that represent resources available to all individuals within a population (Boyce and McDonald 1999, Johnson et al. 2006). We estimated RSFs for Sage-grouse through logistic regression within generalized linear mixed models.

We specified individually radio-marked Sage-grouse, year, and site as random effects in model structures to account for serial and temporal autocorrelation and differences in habitat availability among individual Sage-grouse (Gillies et al. 2006). All models were fit using the lme4 package (Bates et al. 2012) in R (R Core Team 2015). We only measured resource selection on an annual basis owing to a lack of data to adequately model seasonal habitats that can explain substantial variation in annual resource selection (Heinrichs et al. 2017). Habitat availability was defined by first calculating minimum convex polygons (MCP) that encompassed all telemetry locations at each site. All MCPs were then buffered by 1,451 m (i.e., the largest radius used in the moving window analyses that quantified scale-specific availability of habitat features), and five random locations were generated within the MCP boundaries for every used location. Habitat features associated with random locations were then used to estimate available habitat.

Following Coates et al. (2016a), we divided telemetry-location data into three independent data sets that consisted of (1) an RSF model training data set composed of 80% of location data, (2) a classification data set composed of 10% of location data, and (3) a validation data set with the remaining 10% of location data. Individual Sage-grouse were proportionally and randomly assigned to the three data sets. No locations across data sets were shared by the same individual. Using the training data set, we employed a multi-step procedure to carry forward predictor variables to final models that most parsimoniously described variation in Sage-grouse resource selection based on bias-corrected Akaike's information criterion (AIC$_c$; Burnham and Anderson 2002).

In step 1, we grouped predictor variables into corresponding land cover, distance to water source and topographic sets and constructed univariate model sets for each predictor representing competing measurement scales. For each land cover type, we constructed candidate sets composed of percent land cover represented at the three spatial scales (167, 439, and 1,451 m), and carried forward the scale with the lowest AIC$_c$ provided its value was at least 2.0 ΔAIC$_c$ units lower than that of a null (random intercepts only) model. We made one exception to this rule by allowing annual grass to be carried forward owing to its importance to the fire restoration CPT example (see Example applications of CPT). For measurement scales representing distance to water sources (linear and exponential decay) and topographic variables, we carried forward the single best respective scale in each of the two sets provided its model ΔAIC$_c$ was >2.0 units from the null model. We limited the total possible number of models for distance to water source and topographic measurement scale to one per set to reduce the number of variable combinations entered in subsequent steps. No land cover, distance to water source, or topographic predictor variable was carried forward from step 1 if the 95% confidence interval for its parameter estimate included zero.

In step 2, we constructed a set of all possible two-way combinations among the predictor variables carried-forward from step 1 and reduced potential effects of multicollinearity by removing predictor variables that covaried strongly ($r \geq |0.65|$). In this step, understory was collinear with pinyon–juniper, and subsequently removed.

In step 3, we constructed models that included all possible additive combinations of the remaining predictor variables. Owing to the importance of sagebrush to Sage-grouse, all remaining predictor variables representing sagebrush land cover types (i.e., mountain big sagebrush, Wyoming big sagebrush, low sagebrush) were included in all model combinations as an additive group, so no model had fewer than three fixed predictor variables.

In step 4, we sought to account for model uncertainty through weighted averaging across the entire response parameter for each fitted regression model (Cade 2015), whereby each model prediction is multiplied by its respective AIC weight and then summed across all predictions. However, one model garnered the entire AIC weight (see Results), so the final RSF model took the form of

$$w(x) = \exp(\beta_1 X_1 + \beta_2 X_2 + \beta_k X_k) \qquad (1)$$

where $w(x)$ is the predicted relative probability of selection (or RSF) and $\beta_1 \ldots \beta_k$ are the parameter estimates for each covariate ($1 \ldots k$). We excluded β_0 (y-intercept) from predictions because resource availability was estimated rather than censused (Manly et al. 2002). Parameters with 95% confidence intervals overlapping zero also were excluded from predictions, which resulted in the removal of Wyoming big sage as a predictor (95% CI: −0.11 to 0.06). We then applied the RSF to each pixel across the study area extent using the raster package (Hijmans 2015) in R to create a baseline resource selection map from the median parameter coefficients.

To further account for variability in parameter estimates across models that could influence rankings of restoration treatments in the CPT framework (see Example applications of CPT), we created two additional baseline resource selection maps representing "weakest effects" and "strongest effects," by replacing the median parameter coefficients (βs) in Eq. 1 with their respective upper and lower 95% confidence interval limit. Confidence limits with the highest absolute value were used to create the "strongest effects" (i.e., strongest possible selection or avoidance) resource selection map, whereas confidence limits with the lowest absolute value were used to create the "weakest effects" (i.e., most neutral selection or avoidance) resource selection map (Coates et al. 2014a).

We assessed the accuracy of baseline resource selection models using repeated k-fold cross-validation in the caret (Kuhn 2016) and boot (Canty and Ripley 2016) packages for R. Input data were split into 10 subsets for independent training and validation, and the process repeated 30 times. Only fixed effects could be fit to RSF models using this technique. Goodness of mixed-model fit was assessed with marginal and conditional R^2 values (Nakagawa and Schielzeth 2013). We further assessed the accuracy of the predicted baseline resource selection map using methods described by Coates et al. (2015). In brief, the continuous RSF surface

was classified into four discrete categories of habitat selection designated as high, moderate, low, or non-habitat by using standard-deviation-based cut-points derived from the distribution of RSF values characterizing the independent classification set of locations. We then overlaid location data from the independent validation set onto the categorized map, and evaluated agreement between the observed percentage of validation locations falling within each habitat selection category to the predicted percentages (i.e., high ~69%, moderate ~15%, low, ~9%, non-habitat ~7%) based on the shape of the distribution used to categorize the map.

Abundance and space use index.— We used a composite abundance and space-use index (AUI) that combined probabilistic estimates of lek density weighted by abundance (hereafter abundance) with a non-linear probability of space use relative to distance to lek (hereafter space use; Appendix S2: Fig. S4) following the methodology of Coates et al. (2015) and Farzan et al. (2015). Spatial coordinates for leks within the Bi-State and associated counts describing maximum male attendance at leks were obtained from databases compiled by the California Department of Fish and Wildlife and Nevada Department of Wildlife. We included all leks classified as "active" or "pending" over a 10-yr span (2005–2014) in our spatial analyses. Following established protocols (WAFWA 2008), counts were conducted between 1 h before and 2 h after sunrise. Active leks were restricted to leks with at least two consecutive counts of two or more males, while pending leks included leks with no males observed for three consecutive counts or leks that had not been surveyed adequately following a single non-zero count. Pending leks were included in our analysis to allow a greater likelihood of grouse occupancy across the landscape given the uncertainty associated with whether or not a pending lek had actually become inactive.

We indexed Sage-grouse abundance using fixed kernels (Silverman 1986) over lek locations with bandwidths estimated by likelihood based cross-validation (Horne and Garton 2006), which is a commonly used method to delineate population concentrations of Sage-grouse (Doherty et al. 2016). Leks were weighted by their 10-yr average male lek attendance to account for substantial variation in lek size. Hence, larger leks contributed more volume to the estimated utilization distribution than smaller leks. Parameter estimates were calculated using Geospatial Modeling Environment (Beyer 2012) and the ks package in R (Duong 2012), respectively. We estimated patterns of annual space use using a non-linear relationship derived by Coates et al. (2013), representing change in volume of population level utilization distributions with increasing distance to lek. Utilization distributions were centered on the lek and used a radius of 30 km, and the space use index represented the difference between the volume of the utilization distribution value from 1.0 at each cumulative 30 m distance class from the lek. Hence, the lek location received an index value of 1.0, and values declined exponentially as distance from lek increased before flattening at 5–8 km. The AUI was then calculated as the average of Sage-grouse abundance and annual space use indices, relativized to 1.0 by their respective maximum values.

Example applications of CPT

Pinyon–juniper removal.— State and federal agency personnel with local knowledge of their respective management units delineated treatment areas for proposed pinyon–juniper removal. We calculated the baseline RSF surface, and then simulated the effect of pinyon–juniper removal and understory restoration on the post-treatment RSF surface as follows (see Appendix S2: Fig. S5 for flow chart). Importantly, we only simulated removal of low-density and scattered trees within cover-class 1 where the shrub understory is still relatively intact and dominant to trees (Appendix S2: Fig. S2). Importantly, we did not simulate removal of pinyon–juniper co-dominate with shrubs in cover-class 2 or woodland conditions in cover-class 3 (Appendix S2: Fig. S2) owing to high risks of annual grass invasion following disturbance, particularly in areas of low and moderate RR. Furthermore, our pinyon–juniper CPT example assumes that cover-class 1 trees are removed with manual techniques (e.g., hand lop-and-scatter) with low disturbance impacts that minimize risk of annual grass invasion, rather than removal with heavy equipment that have greater disturbance impacts (Tausch et al. 2009, Miller et al. 2014).

Treatment of pinyon–juniper expanding into sagebrush was then simulated in the GIS by removing all pinyon–juniper that intersected class 1 in the cover-class map. Instantaneous restoration of pinyon–juniper understory (i.e., land cover lying beneath cover-class 1) was simulated by returning Landsat-derived understory pixels that intersected removed pinyon–juniper to their original land cover (or the dominant land cover type within 1 km in cases where pixels were classified from Landsat as pinyon–juniper). Moving window analyses were then re-run on land cover types identified in baseline RSF at the model-selected scales to estimate available habitat after pinyon–juniper removal. Baseline RSF coefficients were applied to the post pinyon–juniper removal surface, and resulting RSF values were extracted from treatment areas.

To compare relative changes in habitat suitability, which was performed for median, strongest, and weakest effects separately, baseline and post-pinyon–juniper removal RSF values were first relativized to $\hat{w}$ using a linear stretch described by Johnson et al. (2004) as

$$\hat{w} = (w[x] - w_{min})/(w_{max} - w_{min}). \qquad (2)$$

For the baseline RSF, $w[x]$ is the baseline RSF value at a given pixel, and w_{min} and w_{max} are the minimum and maximum value of the baseline RSF, respectively. The post pinyon–juniper removal RSF was made comparable to the baseline RSF by setting $w[x]$ as the post-removal RSF at a given pixel, while w_{min} and w_{max} remained as the minimum and maximum value of the baseline RSF, respectively. Thus, all changes in RSF values following pinyon–juniper removal were evaluated relative to range of original values in the baseline. We then calculated the ecological benefit to a Sage-grouse as a grouse benefit index (GBI) defined as the difference between the relativized post pinyon–juniper removal and baseline RSF surfaces multiplied by the AUI. We then extracted the sum of GBI values within treatment areas, which represented the total increase in ecological benefit to

Sage-grouse. Economic costs for treatments were set at $432/ha pinyon–juniper cut based on previous pinyon–juniper removal projects conducted in the Bi-State. Benefits (GBI) and costs were relativized by their respective maximum values and treatments were ranked from high to low according to the ratio of total relative GBI to relative total cost (hereafter effective benefit). Finally, we conducted post-hoc comparisons of effective benefits to GIS-estimated reductions in the percentage of pinyon–juniper and increases in sagebrush cover following pinyon–juniper removal, as well as percentages of RR index value composition, across treatment areas using simple linear regression. We used ΔAIC (>2.0) criteria between linear and intercept only models to assess each explanatory variable.

Post-wildfire restoration.—We formulated a spatially explicit decision model for predicting wildfire-driven changes in land cover based on post-fire restoration decisions and underlying soil temperature and moisture regimes influencing RR (Fig. 2). We obtained a sample of wildfire polygons that burned in the Pine Nuts and Bodie Hills region of the Bi-State from 2010 to 2013 and ran the model on a pixel-by-pixel basis. The model first considered variation in normalized burn indices classified with monitoring trends in burn severity methods (Eidenshink et al. 2007), where land cover for pixels with a fire-severity index of 1 remained unchanged (Appendix S2: Fig. S6). Pixels with index values >1 were likely associated with fire severity strong enough to change land cover composition (e.g., kill sagebrush). Thus, we

modeled how decisions to restore or not restore following fire influenced eventual post-fire land cover for these pixels while considering variation in corresponding RR index values (Appendix S2: Fig. S3). Studies (Baker 2011, Miller et al. 2013) suggest that 20% of pre-fire sagebrush conditions can return within 9–15 yr post-fire in highly resilient mountain big sagebrush communities and longer (≥25 yr) in Wyoming big sagebrush communities. Also, 20% shrub cover may provide the minimum cover necessary for some Sage-grouse life history requirements (Connelly et al. 2000, Coates et al. 2016b). Hence, for model simplicity, we assumed that simulated land cover transitions approximated trajectories toward eventual community composition after at least 15 yr post-fire (Coates et al. 2016b). In addition, we modeled outcomes as a general process for broad landscape-level post-fire planning under both scenarios (Restored and Not-Restored), and did not incorporate factors that can influence local restoration success such as differences in slope and aspect, efficacy among different restoration strategies (e.g., broadcast vs. drill seeding, seedling transplants), or fine-scale ecosystem structure (e.g., cover of forbs and perennial grass in shrub-interspaces) (Chambers et al. 2007, Beyer 2012, Arkle et al. 2014, Knutson et al. 2014) not detectable by our coarser Landsat-derived land cover.

To account for this uncertainty, we allowed resistance to annual grass invasion to vary for Restored pixels with low RR, and Not-Restored pixels with moderate and low RR (Fig. 2). These sets of conditions yielded four possible post-fire land cover scenarios calculated for the median,
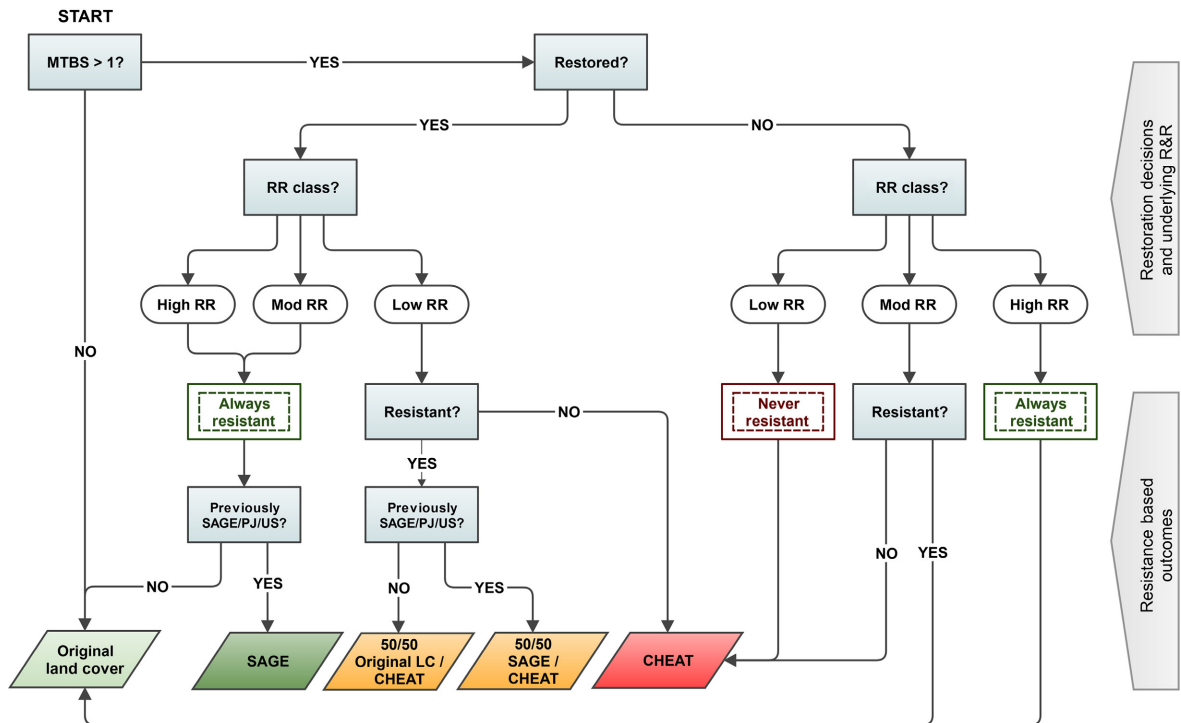

Fig. 2. Diagram of the decision model used to simulate outcomes of restoration decisions on land cover change and subsequent changes in Sage-grouse index (GBI) based on per-pixel (900 m²) variation in fire severity and resilience to disturbance and resistance to invasion (RR) index classes. Local conditions may add uncertainty for resistance to cheatgrass invasion under some moderate and low RR soil temperature and moisture regimes, so the model generates both resistant and not-resistant outcomes in these cases following the decision to restore or not restore. Restored decisions assume active seeding or planting of sagebrush.

strongest, and weakest effects separately: (1) Restored/Resistant; (2) Not-Restored/Resistant; (3) Restored/Not-Resistant; (4) Not-Restored/Not-Resistant. Under the Restored/Resistant scenario, the model simulated active restoration from human intervention activities such as drill seeding and seedling transplants, in contrast with passive restoration driven by successional processes (Pyke 2011) to pre-burn sagebrush land cover types (i.e., mountain big, Wyoming big, or low) in all burned sagebrush habitats. Succession to sagebrush was also simulated in all burned habitats with pinyon–juniper (where we assumed tree expansion into sagebrush had occurred), and the type of sagebrush land cover restored post-fire was based on the majority sagebrush type within 1 km of the burned pinyon–juniper pixel. Restored high and moderate RR pixels were always resistant to annual grass invasion and the model assumed full restoration to sagebrush or return to the original land cover type. In contrast, restored pixels with low RR had an equal probability of full restoration to sagebrush (or return to the original land cover type) vs. invasion by annual grass, which allowed for some level of effectiveness stemming from intense active restoration. Under the Restored/Not-Resistant scenario, outcomes for high and moderate RR pixels remained unchanged, but restored pixels with low RR always converted to annual grass. Under the Not-Restored/Resistant scenario, pixels with high and moderate RR returned to the pre-fire land cover type, while low RR pixels always converted to annual grass. Under the Not-Restored/Not-Resistant scenario, pixels with high RR still returned to the original land cover type, but moderate and low RR pixels always converted to annual grass. Restored/Not-Resistant and Not-Restored/Not-Resistant scenarios yielded identical outcomes for fires that burned over low RR pixels.

We then applied baseline RSF coefficients to each post-fire land cover type scenario (calculated for median, strongest, and weakest effects separately), and ultimately created two GBIs for restored vs. non-restored decisions that were dependent on resistance levels to annual grass invasion. The "Resistant GBI" outcome equaled the difference in GBI between Restored/Resistant and Not-Restored/Resistant land cover scenarios, and the "Not-Resistant GBI" outcome equaled the difference between Restored/Not-Resistant and Not-Restored/Not-Resistant scenarios. Using Eq. 2, we set the Not-Restored scenario as the baseline RSF for respective Resistant and Non-Resistant GBI outcomes. Restored scenarios were then relativized by setting $w[x]$ as the Restored RSF value at given pixel, and w_{min} and w_{max} as the minimum and maximum value of the baseline RSF for respective Resistant and Non-Resistant GBI outcomes. Relativized differences for the Resistant and Not-Resistant outcomes were then multiplied by the AUI, expressed on a per-hectare basis, rescaled by their respective maximum value, and ranked. To represent a composite risk of annual grass invasion relative to restoration decisions and underlying RR index classes, we then averaged GBIs for Resistant (i.e., the least risky outcome) and Not-Resistant (i.e., the most risky) outcomes. Relationships between average GBIs and underlying RR classes, increases in mountain big sagebrush cover, and decreases in annual grass cover were compared using ΔAIC (>2.0) criteria between linear and intercept only models.

RESULTS

Baseline resource selection model

Resource selection for Bi-State Sage-grouse was described by a single model comprising eight predictor variables that accounted for all possible AIC weights ($w = 1.0$) from a set of 127 competing models. Accuracy of the baseline resource selection function as determined from k-fold cross-validation was 0.83, with an adjusted prediction error of 0.11. Fixed effects explained 75.7% of the variance in data (marginal R^2) and random effects explained an additional 1.4% (conditional R^2 − marginal R^2). When the RSF surface was binned into high, moderate, low, and non-habitat categories, the observed percentage (O) of validation points falling within each category matched well with predicted (P) percentages (high$_O$ = 71%, high$_P$ = 69%; moderate$_O$ = 12%, moderate$_P$ = 15%; low$_O$ = 8%, low$_P$ = 9%; non$_O$ = 7%, non$_P$ = 9%).

Parameter estimates from the baseline RSF model (Table 1) indicated exceptionally strong avoidance by Sage-grouse for large expanses of lowland shrub, a community composed of non-sagebrush shrubs, while mountain big sagebrush at the intermediate spatial scale was the most strongly selected land cover type. Notably, avoidance of lowland shrub was substantially greater relative to selection of mountain big sagebrush. Sage-grouse demonstrated avoidance of riparian, pinyon–juniper (intermediate scales), and annual grass (smallest scale). Sage-grouse selected large expanses of low sagebrush. Sage-grouse also selected habitats closer to springs and avoided habitats with rough topography. Confidence limits for parameter estimates used to construct weakest and strongest effects were narrow (<9% of the median effect), except for annual grass and low sagebrush (45%) where median effects were relatively small. Predictions were not made using parameter coefficients for Wyoming big sagebrush (whose effect was modeled additively with the other final model covariates) because its confidence interval overlapped zero.

TABLE 1. Parameter estimates from the top model† used to predict resource selection for Bi-State Sage-grouse.

Parameter	Spatial scale/distance function (ha)	Effect coefficients		
		Median	Weakest	Strongest
Mountain big sagebrush	61	2.66	2.41	2.9
Low sagebrush	661	0.39	0.21	0.56
Pinyon–juniper	61	−3.11	−2.96	−3.25
Lowland shrub	661	−25.78	−23.46	−28.19
Riparian	61	−9.53	−8.40	−10.7
Annual grass	9	−0.79	−0.46	−1.13
Distance to spring	exponential decay‡	1.87	1.76	1.97
Roughness index	1	−9.23	−8.71	−9.76

Note: For each median effect coefficient, weakest effects represent the least positive or negative 95% confidence limit, and strongest effects represent the most positive or negative 95% confidence limit.
†Model contained all of the AIC weight (w_1 = 1.0).
‡Positive coefficient infers selection for exponential decay models.

Pinyon–juniper removal

Fig. 3 illustrates the steps (A–D) used to calculate GBI for proposed pinyon–juniper removal treatments, and the joint influences of relative differences in habitat suitability, as measured by the change in RSF following removal, and lek-centric metrics (AUI) measuring the existing distribution and abundance of Sage-grouse across three representative cases (side panels 1–3). Pinyon–juniper removal alone can result in substantially increased habitat suitability (Fig. 3A and B, side panels 1 and 2). However, the multiplicative effect of these increases in RSF intersected with high AUI (Fig. 3C, side panel 2) yielded the greatest benefits to Sage-grouse (Fig. 3D, side panel 2). In contrast, intersection with low AUI (Fig. 3C, side panel 1) substantially offset benefits from high increases in RSF (Fig. 3D, side panel 1). Weak increases in RSF (Fig. 3A and B, side panel 3) intersected with more moderate AUI (Fig. 3C, side panel 3) generated minimal benefits (Fig. 3D, side panel 3).

The distribution of effective benefit rankings for pinyon–juniper removal was skewed strongly insofar as 10 out of 27 total treatment areas comprised 90% of the cumulative distribution of effective benefit values (Table 2). While more high and moderate RR comprised these top ranked treatments areas on average ($\bar{x} = 60\%$) compared to the remaining bottom-ranked treatment areas ($\bar{x} = 46\%$), variation in effective benefits was unrelated to percentages of high and moderate RR ($\Delta AIC = 0.4$, $R^2 = 0.02$). Notably, the top ranked treatment area included 35% of the cumulative effective benefit distribution, yet was also composed entirely of low RR. However, the next five progressively top ranked treatment areas that included 77% of the cumulative effective benefit distribution had no low RR. Average percentages of pinyon–juniper cut were similar among top ($\bar{x} = 31\%$) and bottom-ranked ($\bar{x} = 27\%$) treatments, and were also unrelated to variation in effective benefits ($\Delta AIC = 1.3$, $R^2 = 0.08$). In contrast, more sagebrush was restored following pinyon–juniper removal treatments ranked in the top ($\bar{x} = 68\%$) compared to the bottom (56%) for cumulative effective benefits. The percentage of restored mountain big sagebrush was related positively to variation in effective benefits ($\Delta AIC = -8.35$, $t = 3.4$, $R^2 = 0.29$).

Importantly, the top and lowest ranked treatment areas had identical percentages of pinyon–juniper cut for the same cost but yielded benefits to Sage-grouse that differed by several orders of magnitude. Variation surrounding median parameter estimates used to calculate strongest and weakest effects had little influence on the overall rank order of treatment areas whereby ranks never differed by more than one place (Table 2).

Post-wildfire restoration

Rankings for Resistant and Not-Resistant outcomes post-wildfire generally mirrored each other, though risks of not restoring in terms of loss of GBI were generally greater under the Not-Resistant outcome as measured by rather large differences in GBI between outcomes (Table 3). Similar to results for pinyon–juniper removal, benefits were skewed strongly toward one wildfire (Spring Peak), which comprised 61% of the cumulative average GBI (average of Resistant and Not-Resistant Outcomes; Table 3). Notably, the Spring Peak fire was comprised almost entirely of high and moderate RR, while the remaining wildfires were dominated by low RR ($\bar{x} = 92\%$). Accordingly, increases in average GBI correlated positively with underlying area of high and moderate RR ($\Delta AIC = -3.5$, $t = 2.4$, $R^2 = 0.30$). Average GBI also correlated positively with increased proportional post-fire area comprised of mountain big sagebrush ($\Delta AIC = -4.0$, $t = 2.5$, $R^2 = 0.33$), but not annual grass ($\Delta AIC = 2.0$, $R^2 = 0.00$). However, average GBI did decrease as the total proportional area invaded by annual grass post-fire increased ($\Delta AIC = -2.3$, $t = -2.1$, $R^2 = 0.23$).

The decision model also had the capacity to identify specific areas for active restoration within a fire perimeter that contained a greater mosaic of RR index classes (Fig. 4). For example, the Bison Fire had the greatest variation in RR, ranked fifth for average GBI, and was one of the largest recorded wildfires in the contemporary history of Nevada. Here, both Resistant and Not-Resistant outcomes, when combined with active restoration, yielded the greatest benefits to Sage-grouse and highest chance of success along the fire's southeastern edge. This example comprised a mix of high and moderate RR pixels modeled as restored to Wyoming and mountain big sagebrush, and was relatively close to a lek (<5 km). In contrast, the northern fire area was almost entirely comprised of low RR with the exception of a narrow strip of high RR along the northwestern edge, and received little influence from the AUI because it was far from a lek (>21 km). Under the Resistant outcome, our model allowed a 50% chance of converting low RR pixels to restored sagebrush, but these pixels also had an equal chance of invasion by annual grass, a habitat feature avoided by Sage-grouse at the smallest scale (9 ha). Hence, relative benefits of restoring the narrow northwestern strip of high RR to sagebrush, which Sage-grouse selected at larger (61 and 661 ha) spatial scales, were diluted by the large patchwork of low RR underlying annual grass and sagebrush habitat directly to the east.

Discussion

We presented a unique approach using the product of empirically derived resource selection, abundance, and space use indices as the currency in a CPT, which can be used to prioritize restoration treatments that provide the greatest ecological benefit for Sage-grouse. It can also be coupled with independent measures of ecosystem resilience to disturbance and resistance to invasion. The result is a powerful tool that uses multiple indices, varying spatial scales, and capacity to combine landscape-level factors that influence the distribution of Sage-grouse leks and Sage-grouse home range (e.g., second-order selection) with resource selection estimates derived from actual patterns of use within an animal's home range (e.g., third-order selection; Johnson 1980). Output from the CPT provides powerful quantitative estimates of treated areas most likely to be used by Sage-grouse given modeled patterns of habitat selection and spatial distribution of Sage-grouse across the landscape. However, we stress that the CPT does not predict how rapidly Sage-grouse may use treated areas or how they will perform demographically after treatments are implemented, and that
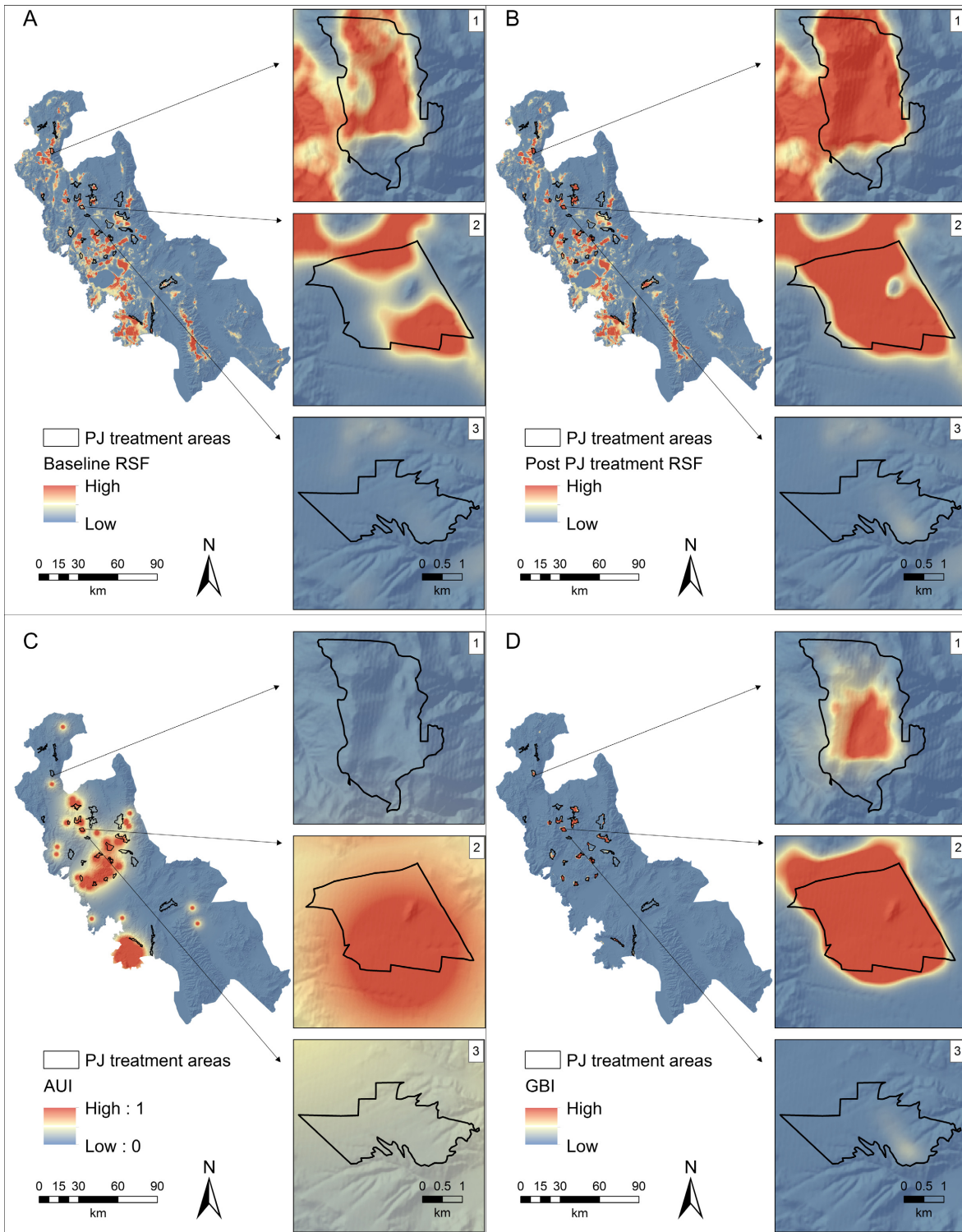
FIG. 3.   Example illustration of taking the difference in resource selection function (RSF) values between (A) baseline and (B) post cover-class 1 pinyon–juniper removal surfaces and (C) multiplying by an intersecting abundance and space use index (AUI) to (D) calculate a grouse benefit index (GBI) to help prioritize areas proposed for pinyon–juniper removal in the Bi-State. Side panels illustrate how high GBI rankings can be driven by high RSF change and low AUI (1), high RSF change and high AUI (2), and low RSF change and moderate AUI (3).

post-treatment monitoring of Sage-grouse ecological and demographic responses are necessary to test the accuracy of CPT predictions and efficacy of the actual treatments.

The CPT's use of multiple indices improves upon concepts used in other SDM-based conservation tools that rely on a single index. For example, SDMs relying solely on

TABLE 2. Areas identified for removal of cover-class 1 pinyon–juniper (0.01–10% canopy cover) in the Bi-State. Areas were ranked based on modeled effective benefits and compared to corresponding sagebrush ecosystem characteristics related to ecological resilience to disturbance and resistance to invasion (RR).

Area of pinyon–juniper cut (ha)	Sage-grouse ecology measures					Sagebrush ecosystem measures				
	Σ GBI increase†	Σ cost‡	Effective benefit§	Cumulative effective benefit (%)	Rank	Pinyon–juniper cut in total treatment area (%)	Total sagebrush post-treatment (%)	High RR (%)	Moderate RR (%)	Low RR (%)
182	516.1	$78,890	4.832	35	1 (1, 1)	23	68	0	0	100
257	218.2	$110,999	1.452	45	2 (2, 2)	37	61	35	64	0
92	67.6	$39,854	1.252	54	3 (3, 4)	15	76	100	0	0
108	79.2	$46,859	1.248	63	4 (4, 3)	32	50	100	0	0
444	299.4	$192,147	1.151	71	5 (5, 5)	44	82	63	37	0
265	128.0	$114,619	0.825	77	6 (6, 7)	48	64	69	31	0
881	390.7	$381,181	0.757	82	7 (7, 6)	22	65	30	52	18
542	152.9	$234,492	0.482	86	8 (8, 8)	39	49	5	0	95
248	50.5	$107,107	0.348	88	9 (9, 10)	24	89	4	3	92
631	113.1	$272,711	0.306	90	10 (11, 9)	27	78	0	3	97
159	25.4	$68,966	0.272	92	11 (12, 11)	18	60	65	31	4
176	27.8	$76,088	0.270	94	12 (10, 12)	40	64	0	13	87
118	14.5	$51,180	0.209	96	13 (13, 13)	24	57	100	0	0
167	11.5	$72,274	0.118	97	14 (14, 16)	19	71	5	32	62
404	26.5	$174,906	0.112	97	15 (16, 14)	20	87	0	0	100
519	33.6	$224,645	0.110	98	16 (15, 15)	26	56	100	0	0
272	11.1	$117,460	0.070	99	17 (17, 18)	56	70	3	97	0
326	11.3	$141,007	0.059	99	18 (18, 17)	25	72	0	0	100
435	11.8	$188,061	0.046	99	19 (19, 19)	28	57	0	5	95
852	16.1	$368,610	0.032	100	20 (20, 20)	23	44	0	2	98
242	2.5	$104,539	0.018	100	21 (21, 21)	43	76	58	42	1
301	2.7	$130,109	0.015	100	22 (22, 22)	14	63	0	17	83
117	0.7	$50,635	0.011	100	23 (23, 23)	25	37	0	0	100
284	1.0	$122,675	0.006	100	24 (24, 24)	24	28	66	28	6
110	0.2	$47,560	0.003	100	25 (25, 25)	21	34	99	1	0
322	0.1	$139,099	0.000	100	26 (26, 27)	31	58	15	3	82
182	0.0	$78,618	0.000	100	27 (27, 26)	23	23	0	0	100

†Total (Σ) increase in GBI (grouse benefit index) following pinyon-juniper removal, defined as the difference between the relativized post pinyon-juniper removal and baseline resource selection function surfaces multiplied by the abundance and space use index.

‡Total cost per treatment, based on $432 per hectare.

§Relative increase in GBI per relative cost for treatment.

Values outside parentheses are ranks resulting from using median RSF parameter estimates. Values inside parentheses are ranks resulting from using weakest and strongest RSF parameter estimates.

TABLE 3. Areas identified for post-wildfire restoration in the Bi-State. Areas were ranked on modeled ecological benefits to sage-grouse (GBI) relative to restoration decision and Resistant and Non-Resistant outcomes, and related to underlying soil conditions influencing sagebrush ecosystem resilience to disturbance and resistance to invasion (RR).

Fire name	Area within burn perimeter (ha)	Burn area with NBR class >1 (%)	Restored – not restored ΔGBI/ha (resistant outcome)	Rank†	Restored – not restored ΔGBI/ha (non-resistant outcome)	Rank†	Average ΔGBI/ha (resistant and non-resistant outcomes)	Rank†	Cumulative average GBI/ha (resistant and non-resistant outcomes)	High RR (%)	Mod RR (%)	Low RR (%)
Spring peak	5,759.4	87	2.18	3 (3,2)	48.80	1 (1,1)	25.49	1 (1,1)	0.61	84	13	1
TRE	2,471.3	62	9.46	1 (1,1)	8.03	3 (3,3)	8.75	2 (2,3)	0.81	0	15	85
Indian	5,088.6	92	2.30	2 (2,3)	8.02	2 (2,2)	5.16	3 (3,2)	0.94	0	40	60
Como	311.1	63	1.93	4 (4,4)	0.00	7 (7,7)	0.96	4 (4,6)	0.96	0	0	100
Bison	9,657.4	89	1.17	6 (6,5)	0.15	4 (4,4)	0.66	5 (5,4)	0.98	15	6	79
Carter springs	1,400.3	76	1.20	5 (5,6)	0.10	5 (5,5)	0.65	6 (6,5)	0.99	0	3	97
Burbank	450.4	83	0.39	7 (7,7)	0.00	7 (7,7)	0.19	7 (7,7)	1.00	0	0	100
Preacher	434.8	81	0.18	8 (8,8)	0.00	7 (7,7)	0.09	8 (8,8)	1.00	0	0	100
Springs	482.5	77	0.13	9 (9,9)	0.00	7 (7,7)	0.07	9 (9,9)	1.00	0	0	100
Laurel	129.6	78	0.00	11 (11,11)	0.00	6 (6,6)	0.00	10 (10,10)	1.00	0	11	89
Rifle	50.2	82	0.01	10 (10,10)	0.00	7 (7,7)	0.00	11 (11,11)	1.00	0	0	100
Weeks	1,563.4	80	0.00	12 (12,12)	0.00	7 (7,7)	0.00	12 (12,12)	1.00	0	0	100

Values outside parentheses are ranks resulting from using median RSF parameter estimates. Values inside parentheses are ranks resulting from using weakest and strongest RSF parameter estimates.

increases in resource selection derived from use vs. availability models do not account for source–sink dynamics in which habitats with disproportionate use do not equate to high productivity (Johnson et al. 2004). Provided data are available, ideal metrics informing the CPT would directly quantify relations between habitat selection and demographic performance (Aldridge and Boyce 2007, Coates et al. 2017b, Heinrichs et al. 2017). However, by incorporating estimates of abundance and space use based on breeding leks typically centered around Sage-grouse nesting activity (Connelly et al. 2000, Coates et al. 2013), the CPT does take into account areas with the greatest potential for habitat improvement near areas where breeding grouse are most likely to occur. In contrast, Farzan et al. (2015) developed a planning tool for Sage-grouse where benefits from management actions were derived solely from intersections with space use, which may not yield the greatest return if landscape features influencing resource selection do not become more available. While the CPT will calculate a relative increase in effective benefits for treatments that are in close proximity to leks but do not improve habitat conditions, it also calculates a similar relative increase when the habitat improves but the treatment is far from a lek. To guard against one index contributing more weight than the other, the CPT multiplies habitat and space use indices, which yields the highest rankings for treatments that have high values for both indices. Last, we demonstrated how CPT output can be either compared (as in the pinyon–juniper example) or directly integrated (as in the post-wildfire restoration example) with more sagebrush ecosystem-centric models based on RR. Considering both measures is essential when identifying and ameliorating threats to Sage-grouse and their habitat (Chambers and Wisdom 2009, Boyd et al. 2014, Chambers et al. 2014c).

Our pinyon–juniper removal example complements recent tools developed by Reinhardt et al. (2017) to help select pinyon–juniper removal sites that are optimal for Sage-grouse. Our example is also particularly germane to applied management of Sage-grouse in the Bi-State and across the Great Basin for several reasons. First, because cost was incorporated into CPT rankings, treatment areas that differ greatly in ecological benefits for Sage-grouse following tree-removal but have equal treatment costs can be identified readily, as was the case with the highest and lowest ranked treatment areas in our example. Thus, the CPT framework can inform the effective allocation of future resources and assist management agencies that have directed significant financial resources towards pinyon–juniper removal to restore sagebrush ecosystems. In addition, the CPT has been identified as a key component for informing habitat restoration for the Bi-State DPS (U.S. Fish and Wildlife Service 2015b). Second, our baseline RSF coefficient for pinyon–juniper demonstrated avoidance by Sage-grouse at the intermediate spatial scale, which corroborates similar findings from other studies (Casazza et al. 2011, Baruch-Mordo et al. 2013, Coates et al. 2017b). Baseline RSF coefficients in our model also indicated selection for all three sagebrush communities, which fits with well-documented patterns of selection for intermediate to large expanses of sagebrush (Connelly et al. 2000, Crawford et al. 2004, Knick et al. 2013). Accordingly, the amount of habitat that returned to
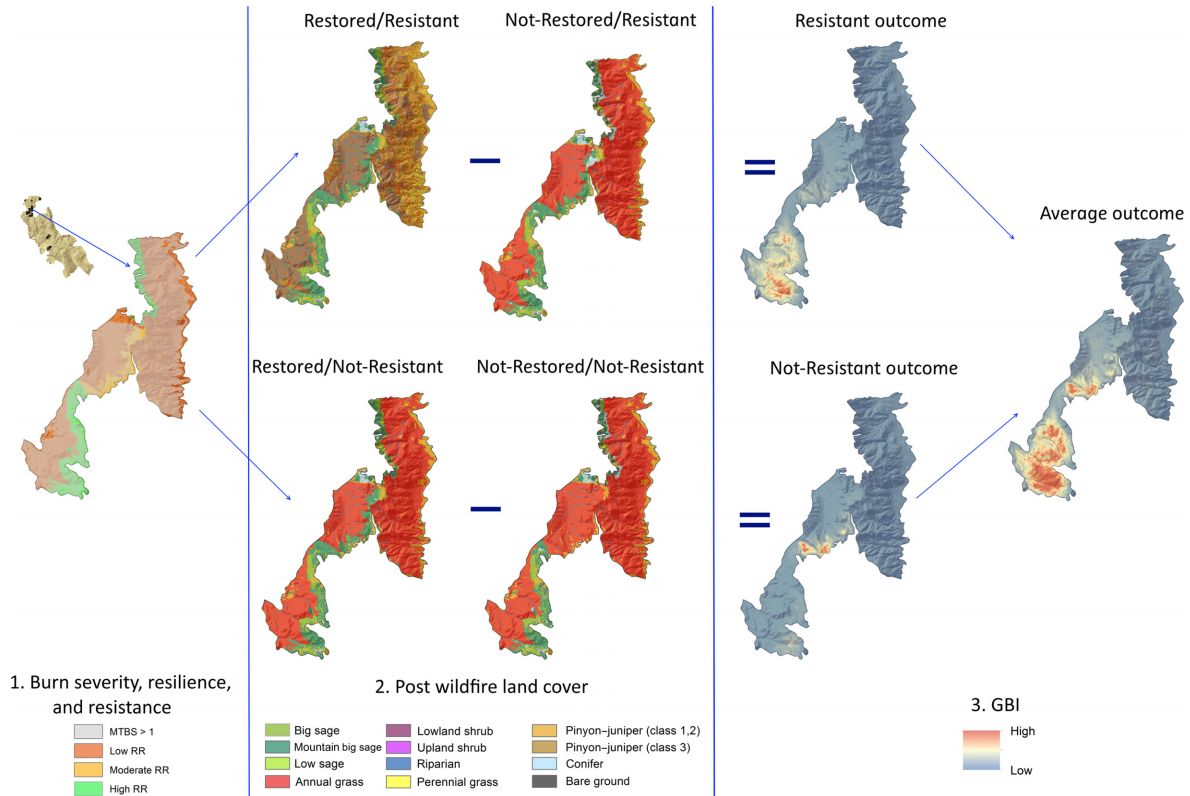
Fig. 4.   Example application of the decision model to the Bison Fire in the northern Bi-State. Variation in monitoring trends in burn severity (MTBS) and underlying soil properties driving resilience to disturbance and resistance to invasion (RR) (panel 1) influence post-wildfire land cover composition (e.g., return or restoration of sagebrush or pre-fire land cover vs. invasion by cheatgrass) following the decision to restore or not restore for Resistant and Not-Resistant outcomes (panel 2). Grouse-benefit index values (GBI) are then calculated for Restoration vs. No Restoration under Resistant and Not-Resistant outcomes, and then averaged (panel 3). Red and blue pixels represent areas where restoration would provide the greatest and least benefit to Sage-grouse, respectively, given varying risk of cheatgrass invasion.

sagebrush following pinyon–juniper removal, particularly large patches of mountain big sagebrush, correlated positively to increases in GBI. In contrast, the actual amount of pinyon–juniper cut was unrelated to changes in GBI. These results suggest that cutting large amounts of pinyon–juniper would be less effective in expansion areas that lack a strong sagebrush understory component (i.e., cover-class or Phase 2 and 3), or with soil conditions not conducive for sagebrush establishment or regeneration (e.g., rocky and shallow soils; Tausch et al. 2009, Miller et al. 2014). Third, post pinyon–juniper removal communities dominated by lowland shrub may be avoided more strongly by Sage-grouse following tree removal owing to the strong negative parameter coefficient for lowland non-sagebrush in our RSF model. Sage-grouse will use lowland shrubs such as rabbitbrush as nesting cover (Crawford et al. 2004, Kolada et al. 2009b), yet large expanses of this cover type do not appear to provide year-round resources for Sage-grouse in the Bi-State. Hence, understory composition needs to be included as a covariate in underlying RSF models used in CPT applications.

Importantly, inferences from our pinyon–juniper removal example rely on key assumptions. First, our classification of cover-class-1 pinyon–juniper from high resolution mapping needed to approximate Phase-1 pinyon–juniper expansion conditions described by Miller et al. (2005) where a shrub

component remains dominant. This assumption was likely robust because all but one treatment area in our analysis was estimated to have an average of 61% sagebrush following pinyon–juniper removal. It follows that treatments of cover-class 1 pinyon–juniper would likely require no or minimal intervention (e.g., seeding or transplanting sagebrush) to restore the shrub component due to the largely intact sagebrush community. Second, we compared, rather than integrated, RR in the pinyon–juniper example because we assumed Phase 1 trees (distributed patchily across sagebrush) would be cut and scattered using low-disturbance methods (e.g., hand lop and scatter). We recognize that differences in RR among proposed treatment areas can influence outcomes of restoration treatments in sagebrush ecosystems (Chambers et al. 2014a). However, the sagebrush community is still intact and has low susceptibility to type conversion to invasive annual grasses following application of low disturbance treatments used to remove Phase 1 trees (Chambers et al. 2014b). Also, if pretreatment cover of perennial grass is low and soil disturbance occurs following tree-removal, resistance to annual grass invasion in low RR areas could be bolstered by seeding or transplanting locally adapted perennials grasses and forbs (Bates et al. 2005, Davies et al. 2011, Miller et al. 2014, Pyke et al. 2017). Treatment areas that provided high ecological benefits per

unit cost to Sage-grouse also matched reasonably well with underlying ecosystem traits that enhance RR (i.e., areas with cool/cold and moist soils). However, when we compared CPT output with RR composition we found instances where selecting areas for pinyon–juniper treatment solely on the basis of moderate to high RR might exclude restoration in low RR areas that could provide substantial benefits to Sage-grouse. In particular, the top rated treatment area in our example accounted for nearly one-third of the cumulative effective benefit, yet it was composed entirely of low RR. This pattern may be related to leks often being located at lower elevations characterized by lower RR in the Bi-State, and Sage-grouse likely do not select habitats based solely on RR conditions. Third, we assumed that removal of pinyon–juniper enhances both RR and Sage-grouse habitat suitability, but the mechanisms behind those enhancements may differ among RR conditions. For example, managing for resilience by removing Phase 1 trees can manifest habitat improvement through multiple pathways such as a reduction of woody fuels and decreased fire severity, improved hydrological conditions, and decreased competition for resources that favor establishment and growth of perennial grasses and shrubs (Bates et al. 2005, Davies et al. 2011, Miller et al. 2014, Pyke et al. 2017). These increases in resilience may be especially important in low RR habitats that often fail to recover following wildfire and comprise a disproportionate amount of the habitat available to Sage-grouse in the Bi-State (Appendix S2: Fig. S3).

Fitness benefits to Sage-grouse following removal of Phase 1 may be dependent on underlying RR conditions. While CPT output can only evaluate benefits to Sage-grouse in terms of increases in habitat suitability, mortality risk to Sage-grouse can increase as they encounter progressively more Phase 1 pinyon–juniper in high vs. low RR habitats (Coates et al. 2017b). Phase 1 pinyon–juniper expansion in high RR habitats may constitute an ecological trap (Robertson and Hutto 2006, Aldridge and Boyce 2007) for Sage-grouse that are drawn to abundant resources but may not perceive higher mortality risk likely due to presence of avian predators perched in scattered trees (Coates et al. 2017b). Thus removal of Phase 1 may be particularly important in montane and mesic habitats selected for brood rearing (Coates et al. 2017b). Last, risks of annual grass invasion can increase following large-scale treatments of Phase 1 pinyon–juniper with heavy machinery, or removal of Phase 2 or Phase 3 pinyon–juniper where sagebrush and herbaceous vegetation are insufficient to facilitate recovery. Accordingly, CPT models applied using these types of high-disturbance treatments should directly incorporate RR into site rankings.

While CPT output for pinyon–juniper removal in our example can be used to compare Sage-grouse and sagebrush ecosystem responses to restoration, the decision model used in the fire CPT directly incorporated Sage-grouse-centric GBI and sagebrush ecosystem centric RR. Specifically, the fire CPT evaluated resource and spatial use responses of Sage-grouse in four post-fire landscapes simulated from the decision model based on soil temperature and moisture regimes driving RR. Fire CPT output indicated that restoration of habitats with high and moderate RR yielded a higher return of sagebrush (particularly mountain big sagebrush)

and provided greater ecological benefit to Sage-grouse than restoration in low RR habitats. Also, intense active restoration efforts in low RR habitats that result in a patchwork of success (i.e., Restored/Resistant outcomes) yield little benefit because Sage-grouse select sagebrush at large spatial scales and avoid annual grass at small spatial scales, and benefits are more diminished in areas far away from leks. Restoring isolated patches of high RR habitat adjacent to large patches of annual grass in the Bison fire example also further illustrated patterns depicted by the pinyon–juniper example whereby restoration decisions based on both Sage-grouse and sagebrush ecology yielded benefits to Sage-grouse.

The conditional parameters used to model post-fire land cover composition in the decision model include broad assumptions, yet these parameters may be modified to simulate return to more ecologically complex land cover types. For example, sagebrush return in restored burned pinyon–juniper habitats may not occur, especially if disturbance thresholds associated with transitions from Phase 2 to Phase 3 woodlands have been surpassed (Miller et al. 2005, Strand et al. 2013). Factors such as restoration method efficacy (Arkle et al. 2014, Knutson et al. 2014), seed source (Eiswerth et al. 2009), and site evaluation of disturbance severity (e.g., perennial grass mortality; Miller et al. 2008, Condon et al. 2011) can also be incorporated into the conditional parameters provided they are spatially explicit. In addition, avoidance of cheatgrass was likely underestimated in our RSF model owing largely to low abundance of cheatgrass in the Bi-State compared to the rest of the Great Basin. The fire CPT gave less weight to low resistance outcomes predicting cheatgrass invasion in moderate or low RR soil regimes, and more weight to resilient and resistant outcomes predicting successful sagebrush communities that had larger and positive RSF coefficients. Higher resolution cheatgrass GIS layers, particularly those for shrub interspaces and sub-900-m^2 spatial scales, should improve predictability for effects of cheatgrass invasion on Sage-grouse resource selection. Similarly, greater spatial variation in soil temperature and moisture can be modeled by subdividing the relatively course RR map comprised of three categories into finer categories depicting soil temperature and soil moisture sub-classes and topographic aspect that allow modeling scenarios of post-wildfire land cover at higher spatial resolutions. While these complexities were not addressed by the conditional model parameters predicting post-wildfire changes in land cover, a strength of the CPT for fire restoration lies in its use of the change in GBI as the currency for evaluating benefits of management actions to Sage-grouse, which can be further evaluated under a multitude of restoration outcomes based on variations of RR and plant community response. Moreover, the abundance and space use indices built into the GBI help target restoration in areas where Sage-grouse likely occur.

The utility of our CPT framework that uses the change in GBI as the measure for management action efficacy is not limited to the Bi-State DPS. Rather, it can be extended to other Sage-grouse populations across the range of the species to help evaluate proposed management actions. As part of hierarchical decision making by managers, the CPT framework can be scaled up to guide pinyon–juniper removal across larger geographic regions using high

resolution conifer mapping products developed for much of the contemporary range of Sage-grouse (Falkowski et al. 2017), and coupled with regionally appropriate Sage-grouse resource selection and distribution indices. The concept can also be used as a quantitative "first cut" to evaluate efficacy of proposed management actions across landscape scales with generalized assumptions regarding underlying factors influencing RR. Management options can then be refined further with finer scale information related to ecological factors that can modify RR specific to each site, and could include spatially explicit input data from field measurements of sagebrush interspace gaps, perennial grass and forb cover, biological soil crust integrity, and grazing intensity. Approaches for mitigating effects for other disturbances can also be modeled with the CPT framework. For example, power-transmission lines will likely occupy a larger footprint across the Great Basin as renewable energy sources (e.g., solar, geothermal) increase in production. Infrastructure associated with energy development can diminish habitat quality for Sage-grouse (Coates et al. 2014b, Howe et al. 2014), and the CPT framework can be used to help guide placement of energy transmission routes in areas that will minimize impacts to Sage-grouse. Also, effects from future changes in precipitation and temperature could be evaluated using changes in GBI, such as drying of springs and seeps that provide important brood-rearing habitat and contribute strongly to the RSF portion of the GBI.

Moreover, now that the foundation for using multiple indices to measure benefits to Sage-grouse has been established, future versions of the CPT can become more powerful by incorporating spatially explicit measures of variation in fitness parameters. For example, relative risk maps depicting how habitat covariates influence nesting and brood survival that help bypass potential pitfalls associated with inferring habitat quality from selection and occupancy could be incorporated into CPTs (Aldridge and Boyce 2007, Heinrichs et al. 2017), as could measures of landscape resistance to gene flow (Row et al. 2015). In these scenarios, indices measuring changes to individual and population-level fitness and genetics from proposed pinyon–juniper and wildfire restoration projects could then be used in an overall index of ecological benefits to Sage-grouse. Additional benefits might be found by considering how Sage-grouse respond spatially and demographically to restoration patch size and configuration. In short, the fundamental CPT framework we present here can be customized to include forthcoming insights into Sage-grouse biology and conservation.

Finally, effectiveness of management actions across larger landscape scales increases greatly by pairing species ecology with ecosystem attributes within the context of the CPT. Our results illustrate that sagebrush ecosystem and Sage-grouse ecology are linked intricately and suggest that Sage-grouse and ecological community responses to management actions are best evaluated together and not in isolation (Chambers and Wisdom 2009, Boyd et al. 2014). The CPT framework we present can also be applied to many species with space use attributes similar to Sage-grouse, such as central-place breeding, and that occupy complex habitat mosaics where underlying processes influencing RR are well understood.

LITERATURE CITED

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered Greater Sage-Grouse. Ecological Applications 17:508–526.

Aldridge, C. L., D. J. Saher, T. M. Childers, K. E. Stahlnecker, and Z. H. Bowen. 2012. Crucial nesting habitat for Gunnison sage-grouse: a spatially explicit hierarchical approach. Journal of Wildlife Management 76:391–406.

Arkle, R. S., D. S. Pilliod, S. E. Hanser, M. L. Brooks, J. C. Chambers, J. B. Grace, K. C. Knutson, D. A. Pyke, J. L. Welty, and T. A. Wirth. 2014. Quantifying restoration effectiveness using multi-scale habitat models: implications for sage-grouse in the Great Basin. Ecosphere 5:art31.

Atamian, M. T., J. S. Sedinger, J. S. Heaton, and E. J. Blomberg. 2010. Landscape-level assessment of brood rearing habitat for Greater Sage-Grouse in Nevada. Journal of Wildlife Management 74:1533–1543.

Baker, W. L. 2011. Pre-Euro-American and recent fire in sagebrush ecosystems. Pages 185–201 in S. T. Knick and J. W. Connelly, editors. Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats. University of California Press, Berkeley, California, USA.

Balch, J. K., B. A. Bradley, C. M. D'Antonio, and J. Gómez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). Global Change Biology 19:173–183.

Baruch-Mordo, S., J. S. Evans, J. P. Severson, D. E. Naugle, J. D. Maestas, J. M. Kiesecker, M. J. Falkowski, C. A. Hagen, and K. P. Reese. 2013. Saving sage-grouse from the trees: a proactive solution to reducing a key threat to a candidate species. Biological Conservation 167:233–241.

Bates, J. D., R. F. Miller, and T. Svejcar. 2005. Long-term successional trends following western juniper cutting. Rangeland Ecology and Management 58:533–541.

Bates, D., M. Maechler, and B. Bolker. 2012. lme4: Linear mixed-effects models using S4 classes. R package version 3.0.2. http://CRAN.R-project.org/package=lme4

Benedict, N. G., S. J. Oyler-McCance, S. E. Taylor, C. E. Braun, and T. W. Quinn. 2003. Evaluation of the eastern (Centrocercus urophasianus urophasianus) and western (Centrocercus urophasianus phaios) subspecies of Sage-grouse using mitochondrial control-region sequence data. Conservation Genetics 4:301–310.

Beyer, H. L. 2012. Geospatial Modelling Environment. version 0.7.2.0. http://www.spatialecology.com/gme

Bi-State-Action-Plan. 2012. Bi-State action plan: past, present, and future actions for conservation of the greater sage-grouse Bi-State Distinct Population Segment. Prepared by the Bi-State Technical Advisory Committee (Nevada and California) for the Bi-State Executive Oversight Committee for Conservation of Greater Sage-Grouse. http://sagebrushco.nv.gov/uploadedfiles/sagebrusheconvgov/content/archive/bi-stateactionplan2012.pdf

Blomberg, E. J., J. S. Sedinger, M. T. Atamian, and D. V. Nonne. 2012. Characteristics of climate and landscape disturbance influence the dynamics of greater sage-grouse populations. Ecosphere 3:art55.

Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14:268–272.

Boyd, C. S., D. D. Johnson, J. D. Kerby, T. J. Svejcar, and K. W. Davies. 2014. Of grouse and golden eggs: Can ecosystems be managed within a species-based regulatory framework? Rangeland Ecology and Management 67:358–368.

Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. BioScience 54:677–688.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. Second edition. Springer, New York, New York, USA.

Cade, B. S. 2015. Model averaging and muddled multimodel inference. Ecology 96:2370–2382.

Canty, A., and B. Ripley. 2016. boot: Bootstrap functions (originally by A. Canty for S). R package version 1.3-18. http://CRAN.R-pro ject.org/package=boot

Casazza, M. L., P. S. Coates, and C. T. Overton. 2011. Linking habitat selection and brood success in Greater Sage-Grouse. Pages 151–167 in B. K. Sandercock, K. Martin, and G. Segelbacher, editors. Ecology, conservation, and management of grouse. Studies in Avian Biology (no. 39). University of California Press, Berkeley, California, USA.

U.S. Fish and Wildlife Service. 2010. Endangered and threatened wildlife and plants; 12-month findings for petitions to list the greater sage-grouse (Centrocercus urophasianus) as threatened or endangered. Federal Register 75:13910–141014.

U.S. Fish and Wildlife Service. 2013. Endangered and threatened wildlife and plants; threatened status for the Bi-State Distinct Population Segment of greater sage-grouse with special rule. Federal Register 78:64358–64384.

U.S. Fish and Wildlife Service. 2015a. Endangered and Threatened Wildlife and Plants; 12-Month finding on a petition to list greater sage-grouse (Centrocercus urophasianus) as an endangered or threatened species. Federal Register 80:59858–59942.

U.S. Fish and Wildlife Service. 2015b. Endangered and threatened wildlife and plants; withdrawal of proposed rule to list the Bi-State Distinct Population Segment of greater sage-grouse and designate critical habitat. Federal Register 80:22828–22866.

Chambers, J. C., and M. J. Wisdom. 2009. Priority research and management issues for the imperiled Great Basin of the Western United States. Restoration Ecology 17:707–714.

Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invasible by Bromus tectorum? Ecological Monographs 77:117–145.

Chambers, J. C., B. A. Bradley, C. S. Brown, C. D'Antonio, M. J. Germino, J. B. Grace, S. P. Hardegree, R. F. Miller, and D. A. Pyke. 2014a. Resilience to stress and disturbance, and resistance to Bromus tectorum L. invasion in cold desert shrublands of Western North America. Ecosystems 17:360–375.

Chambers, J. C., R. F. Miller, D. I. Board, D. A. Pyke, B. A. Roundy, J. B. Grace, E. W. Schupp, and R. J. Tausch. 2014b. Resilience and resistance of sagebrush ecosystems: implications for state and transition models and management treatments. Rangeland Ecology and Management 67:440–454.

Chambers, J. C., D. A. M. Pyke, J. D. Pellant, C. S. Boyd, S. B. Campbell, S. P. Espinosa, D. W. Havlina, K. E. Mayer, and A. Wuenschel. 2014c. Using resistance and resilience concepts to reduce impacts of invasive annual grasses and altered fire regimes on the sagebrush ecosystem and greater sage-grouse: a strategic multi-scale approach. General Technical Report RMRS-GTR-326. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA. http://www.fs.fed.us/rm/pubs/rmrs_gtr326.pdf

Coates, P. S., and D. J. Delehanty. 2008. Effects of environmental factors on incubation patterns of greater sage-grouse. Condor 110:627–638.

Coates, P. S., and D. J. Delehanty. 2010. Nest predation of greater sage-grouse in relation to microhabitat factors and predators. Journal of Wildlife Management 74:240–248.

Coates, P. S., M. L. Casazza, E. J. Blomberg, S. C. Gardner, S. P. Espinosa, J. L. Yee, L. Wiechman, and B. J. Halstead. 2013. Evaluating greater sage-grouse seasonal space use relative to leks: Implications for surface use designations in sagebrush ecosystems. Journal of Wildlife Management 77:1598–1609.

Coates, P. S., K. B. Howe, M. L. Casazza, and D. J. Delehanty. 2014a. Common raven occurrence in relation to energy transmission line corridors transiting human-altered sagebrush steppe. Journal of Arid Environments 111:68–78.

Coates, P. S., K. B. Howe, M. L. Casazza, and D. J. Delehanty. 2014b. Landscape alterations influence differential habitat use of nesting buteos and ravens within sagebrush ecosystem: implications for transmission line development. Condor 116:341–356.

Coates, P. S., et al. 2015. Integrating spatially explicit indices of abundance and habitat quality: an applied example for greater sage-grouse management. Journal of Applied Ecology 53:83–95.

Coates, P. S., et al. 2016a. Integrating spatially explicit indices of abundance and habitat quality: an applied example for greater sage-grouse management. Journal of Applied Ecology 53:83–95.

Coates, P. S., M. A. Ricca, B. G. Prochazka, M. L. Brooks, K. E. Doherty, T. Kroger, E. J. Blomberg, C. A. Hagen, and M. L. Casazza. 2016b. Wildfire, climate, and invasive grass interactions negatively impact an indicator species by reshaping sagebrush ecosystems. Proceedings of the National Academy of Sciences USA 113:12745–12750.

Coates, P. S., K. B. Gustafson, C. L. Roth, M. P. Chenaille, M. A. Ricca, K. Mauch, E. Sanchez-chopitea, T. J. Kroger, W. M. Perry, and M. L. Casazza. 2017a. Using object-based image analysis to conduct high-resolution conifer extraction at regional spatial scales. U.S. Geological Survey Open-File Report 2017-1093, Reston, Virginia, USA. http://pubs.er.usgs.gov/publication/ofr2017 1093

Coates, P. S., B. G. Prochazka, M. A. Ricca, K. B. Gustafson, P. Ziegler, and M. L. Casazza. 2017b. Pinyon and juniper encroachment into sagebrush ecosystems impacts distribution and survival of greater sage-grouse. Rangeland Ecology and Management 70:25–38.

Coates, P. S., B. G. Prochazka, M. A. Ricca, B. J. Halstead, M. L. Casazza, E. J. Blomberg, B. E. Brussee, L. Wiechman, J. Tebben-kamp, S. C. Gardner, and K. P. Reese, 2018. The relative importance of intrinsic and extrinsic drivers to population growth vary among local populations of Greater Sage-Grouse: an integrated population modeling approach. Auk: Ornithological Advances 135:240–261.

Condon, L., P. J. Weisberg, and J. C. Chambers. 2011. Abiotic and biotic influences on Bromus tectorum invasion and Artemisia tridentata recovery after fire. International Journal of Wildland Fire 20:597–604.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967–985.

Crawford, J. A., R. A. Olson, N. E. West, J. C. Mosley, M. A. Schroeder, T. D. Whitson, R. F. Miller, M. A. Gregg, and C. S. Boyd. 2004. Ecology and management of sage-grouse and sage-grouse habitat. Journal of Range Management 57:2–19.

Dalke, P. D., B. Pyrah, D. C. Stanton, J. E. Crawford, and E. F. Schlatterer. 1963. Ecology, productivity, and management of sage grouse in Idaho. Journal of Wildlife Management 27:810–841.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23:63–87.

Davies, K. W., C. S. Boyd, J. L. Beck, J. D. Bates, T. J. Svejcar, and M. A. Gregg. 2011. Saving the sagebrush sea: an ecosystem

conservation plan for big sagebrush plant communities. Biological Conservation 144:2573–2584.

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

Doherty, K. E., D. E. Naugle, H. E. Copeland, A. Pocewicz, and J. M. Kiesecker. 2011. Energy development and conservation trade-offs: systematic planning for Greater Sage-Grouse in their eastern range. Pages 505–516 in S. T. Knick and J. W. Connelly, editors. Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology. University of California Press, Berkeley, California, USA.

Doherty, K. E., J. S. Evans, P. S. Coates, L. M. Juliusson, and B. C. Fedy. 2016. Importance of regional variation in conservation planning: a rangewide example of the Greater Sage-Grouse. Ecosphere 7:e01462.

Duong, T. 2012. ks: Kernel smoothing. R package version 1.8.10. http://CRAN.R-project.org/package=ks

Dzialak, M. R., C. V. Olson, S. M. Harju, S. L. Webb, and J. B. Winstead. 2012. Temporal and hierarchical spatial components of animal occurrence: conserving seasonal habitat for greater sage-grouse. Ecosphere 3:art30.

Eidenshink, J., B. Schwind, K. Brewer, Z. L. Zhu, B. Quayle, and S. Howard. 2007. A project for monitoring trends in burn severity. Fire Ecology 3:3–22.

Eiswerth, M. E., K. Krauter, S. R. Swanson, and M. Zielinski. 2009. Post-fire seeding on Wyoming big sagebrush ecological sites: regression analyses of seeded nonnative and native species densities. Journal of Environmental Management 90:1320–1325.

Falkowski, M. J., J. S. Evans, D. E. Naugle, C. A. Hagen, S. A. Carleton, J. D. Maestas, A. H. Khalyani, A. J. Poznanovic, and A. J. Lawrence. 2017. Mapping tree canopy cover in support of proactive prairie grouse conservation in western North America. Rangeland Ecology and Management 70:15–24.

Farzan, S., D. Young, A. Dedrick, M. Hamilton, E. Porse, P. S. Coates, and G. Sampson. 2015. Western juniper management: assessing policies for improving greater sage-grouse habitat and rangeland productivity. Journal of Environmental Management 56:675–683.

Fedy, B. C., et al. 2012. Interseasonal movements of greater sage-grouse, migratory behavior, and an assessment of the core regions concept in Wyoming. Journal of Wildlife Management 76:1062–1071.

Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology, Evolution, and Systematics 35:557–581.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75:887–898.

Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135:147–186.

Guisan, A., A. Lehmann, S. Ferrier, M. Austin, J. M. C. Overton, R. Aspinall, and T. Hastie. 2006. Making better biogeographical predictions of species' distributions. Journal of Applied Ecology 43:386–392.

Guisan, A., et al. 2013. Predicting species distributions for conservation decisions. Ecology Letters 16:1424–1435.

Heinrichs, J. A., C. L. Aldridge, M. S. O'Donnell, and N. H. Schumaker. 2017. Using dynamic population simulations to extend resource selection analyses and prioritize habitats for conservation. Ecological Modelling 359:449–459.

Hijmans, R. J. 2015. raster: geographic data analysis and modeling. R package version 2.4-15. http://CRAN.R-project.org/package=raster

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1–23.

Horne, J. S., and E. O. Garton. 2006. Selecting the best home range model: an information-theoretic approach. Ecology 87:1146–1152.

Howe, K. B., P. S. Coates, and D. J. Delehanty. 2014. Selection of anthropogenic features and vegetation characteristics by nesting Common Ravens in the sagebrush ecosystem. Condor 116:35–49.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Johnson, C. J., and M. P. Gillingham. 2005. An evaluation of mapped species distribution models used for conservation planning. Environmental Conservation 32:117–128.

Johnson, C. J., D. R. Seip, and M. S. Boyce. 2004. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. Journal of Applied Ecology 41:238–251.

Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. Journal of Wildlife Management 70:347–357.

Kirol, C. P., J. L. Beck, J. B. Dinkins, and M. R. Conover. 2012. Microhabitat selection for nesting and brood-rearing by the greater sage-grouse in xeric big sagebrush. Condor 114:75–89.

Knick, S. T., S. E. Hanser, and K. L. Preston. 2013. Modeling ecological minimum requirements for distribution of greater sage-grouse leks: implications for population connectivity across their western range, U.S.A. Ecology and Evolution 3:1539–1551.

Knutson, K. C., D. A. Pyke, T. A. Wirth, R. S. Arkle, D. S. Pilliod, M. L. Brooks, J. C. Chambers, and J. B. Grace. 2014. Long-term effects of seeding after wildfire on vegetation in Great Basin shrubland ecosystems. Journal of Applied Ecology 5:1414–1424.

Kolada, E. J., M. L. Casazza, and J. S. Sedinger. 2009a. Ecological factors influencing nest survival of greater sage-grouse in Mono County, California. Journal of Wildlife Management 73:1341–1347.

Kolada, E. J., J. S. Sedinger, and M. L. Casazza. 2009b. Nest site selection by greater sage-grouse in Mono County, California. Journal of Wildlife Management 73:1333–1340.

Kuhn, M. 2016. caret: Classification and Regression Training. R package version 6.0-68. http://CRAN.R-project.org/package=caret

Lockyer, Z. B., P. S. Coates, M. L. Casazza, S. Espinosa, and D. J. Delehanty. 2015. Nest-site selection and reproductive success of greater sage-grouse in a fire-affected habitat of northwestern Nevada. Journal of Wildlife Management 79:785–797.

Maestas, J. D., S. B. Campbell, J. C. Chambers, M. Pellant, and R. F. Miller. 2016. Tapping soil survey information for rapid assessment of sagebrush ecosystem resilience and resistance. Rangelands 38:120–128.

Manly, B. F., L. L. McDonald, D. L. Thomas, L. McDonald, and P. E. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Chapman and Hall, London, UK.

Miller, R. F., J. D. Bates, T. J. Svejcar, F. B. Pierson, and L. E. Eddleman. 2005. Biology, ecology, and management of western juniper. Technical Bulletin 152. Oregon State University Agricultural Experiment Station, Corvallis, Oregon, USA. http://juniper.oregonstate.edu/bibliography/documents/phpQ65pOk_tb152.pdf

Miller, R. F., R. J. Tausch, E. Durant MacArthur, D. D. Johnson, and S. C. Sanderson. 2008. Age structure and expansion of piñon-juniper woodlands: a regional perspective in the Intermountain West. Research Paper RMRS-RP-69. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Miller, R. F., S. T. Knick, D. A. Pyke, C. W. Meinke, S. E. Hanser, M. J. Wisdom, and A. L. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Pages 145–184 in S. T. Knick and J. W. Connelly, editors. Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats. University of California Press, Berkeley, California, USA.

Miller, R. F., J. C. Chambers, D. A. Pyke, F. B. Pierson, and C. J. Williams. 2013. A review of fire effects on vegetation and soils in the Great Basin Region: response and ecological site characteristics. Gen. Tech. Rep. RMRS-GTR-308. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station,

Fort Collins, Colorado, USA. http://www.fs.fed.us/rm/pubs/rmrs_gtr308.html

Miller, R. F., J. C. Chambers, and M. Pellant. 2014. A field guide for selecting the most appropriate treatment in sagebrush and piñon-juniper ecosystems in the Great Basin: evaluating resilience to disturbance and resistance to invasive annual grasses, and predicting vegetation response. General Technical Report RMRS-GTR-322. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133–142.

Nielsen, S. E., J. Cranston, and G. B. Stenhouse. 2009. Identification of priority areas for grizzly bear conservation and recovery in Alberta, Canada. Journal of Conservation Planning 5:38–60.

Noss, R. F., M. A. O'Connell, and D. D. Murphy. 1997. The science of conservation planning: habitat conservation under the Endangered Species Act. Island Press, Washington, D.C., USA.

Oyler-McCance, S. J., R. S. Cornman, K. L. Jones, and J. A. Fike. 2015. Genomic single-nucleotide polymorphisms confirm that Gunnison and Greater sage-grouse are genetically well differentiated and that the Bi-State population is distinct. Condor 117:217–227.

Prochazka, B. G., P. S. Coates, M. A. Ricca, M. L. Casazza, and J. M. Hull. 2017. Encounters with pinyon–juniper influence riskier movements in greater sage-grouse across the Great Basin. Rangeland Ecology and Management 70:39–49.

Pulliam, H. R. 2000. On the relationship between niche and distribution. Ecology Letters 3:349–361.

Pyke, D. A. 2011. Restoring and rehabilitating sagebrush habitats. Pages 531–548 in S. T. Knick and J. W. Connelly, editors. Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats. University of California Press, Berkeley, California, USA.

Pyke, D. A., et al. 2017. Restoration handbook for sagebrush steppe ecosystems with emphasis on greater sage-grouse habitat—Part 3. Site level restoration decisions. U.S. Geological Survey Circular 1426. Reston, Virginia, USA. https://doi.org/10.3133/cir1426.

R Core Team. 2015. R: A language and environment for statistical computing. Version 3.13. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Reinhardt, J. R., D. E. Naugle, J. D. Maestas, B. Allred, J. Evans, and M. Falkowski. 2017. Next-generation restoration for sage-grouse: a framework for visualizing local conifer cuts within a landscape context. Ecosphere 8:e01888.

Robertson, B. A., and R. L. Hutto. 2006. A framework for understanding ecological traps and an evaluation of existing evidence. Ecology 87:1075–1085.

Romme, W. H., et al. 2009. Historical and modern disturbance regimes, stand structures, and landscape dynamics in pinon-juniper vegetation of the Western United States. Rangeland Ecology and Management 62:203–222.

Row, J. R., S. J. Oyler-McCance, J. A. Fike, M. S. O'Donnell, K. E. Doherty, C. L. Aldridge, Z. H. Bowen, and B. C. Fedy. 2015. Landscape characteristics influencing the genetic structure of greater sage-grouse within the stronghold of their range: a holistic modeling approach. Ecology and Evolution 5:1955–1969.

Rowland, M. M., M. J. Wisdom, L. H. Suring, and C. W. Meinke. 2006. Greater sage-grouse as an umbrella species for sagebrush-associated vertebrates. Biological Conservation 129:323–335.

Rushton, S. P., S. J. Ormerod, and G. Kerby. 2004. New paradigms for modelling species distributions? Journal of Applied Ecology 41:193–200.

Schroeder, M. A., et al. 2004. Distribution of sage-grouse in North America. Condor 106:363–376.

Severson, J. P., C. A. Hagen, J. D. Maestas, D. E. Naugle, J. T. Forbes, and K. P. Reese. 2017. Effects of conifer expansion on greater sage-grouse nesting habitat selection. Journal of Wildlife Management 81:86–95.

Silverman, B. 1986. Density estimation for statistics and data analysis. Chapman and Hall, London, UK.

Standish, R. J., et al. 2014. Resilience in ecology: Abstraction, distraction, or where the action is? Biological Conservation 177:43–51.

Stephens, P. A., N. Pettorelli, J. Barlow, M. J. Whittingham, and M. W. Cadotte. 2015. Management by proxy? The use of indices in applied ecology. Journal of Applied Ecology 52:1–6.

Strand, E. K., S. C. Bunting, and R. F. Keefe. 2013. Influence of wildland fire along a successional gradient in sagebrush steppe and western juniper woodlands. Rangeland Ecology and Management 66:667–679.

Tausch, R. J., F. L. Miller, B. A. Roundy, and J. C. Chambers. 2009. Piñon and juniper field guide: asking the right questions to select appropriate management actions. U.S. Geological Survey Circular 1335. U.S. Geological Survey, Reston, Virginia, USA.

WAFWA. 2008. Greater Sage-Grouse population trends: an analysis of lek count databases 1965–2007. Sage and Columbian Sharp-tailed Grouse Technical Committee, Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.

Wakkinen, W. L., K. P. Reese, and J. W. Connelly. 1992. Sage grouse nest locations in relation to leks. Journal of Wildlife Management 56:381–383.

Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. Journal of Range Management 42:266–274.

Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1690/full

Data Availability

Data available from the USGS ScienceBase Repository: https://doi.org/10.5066/f7tt4q5s.