Wildlife Society Bulletin 45(3):473–487; 2021; DOI: 10.1002/wsb.1200

THE WILDLIFE SOCIETY

Research Article

Threat-Based State and Transition Models Predict Sage-Grouse Occurrence while Promoting Landscape Conservation

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ABSTRACT A recent collaboration between federal, state and private partners in southeast Oregon developed mental models to distill complex plant-based community ecology for management. The mental models were then turned into a simplified, habitat-classification system that addressed landscape-level threats to the sagebrush ecosystem. The simplified, habitat-classification system formed the foundation of Threat-based State and Transition Models (TBSTM). We quantitatively linked greater sage-grouse (*Centrocercus urophasianus*, hereafter sage-grouse) lek occurrence to a landscape-level habitat classification based upon the TBSTM framework. We investigated whether TBSTM classifications were able to spatially predict locations of sage-grouse breeding areas equivalently to landcover variables that have been studied for over a decade. We showed the TBSTM framework was able to predict the locations of sage-grouse accurately ($R^2 = 0.70$, AUC = 0.91, Correctly Classified = 83%). Model fit statistics were similar to the model built with traditional land cover variables ($R^2 = 0.65$, AUC = 0.89, Correctly Classified = 80%). The high degree of model fit for the TBSTM framework allows conservation practitioners a direct, quantifiable, and biological link to understand outcomes of transitioning habitats from various threat states to sagebrush-dominated landscapes with a perennial understory across large landscapes. Sage-grouse are well known to respond to landscape-level amounts of habitat and exhibit low tolerance to threats. We documented similar responses between threats such as the percentage of conifers within 560-m and the conifer threat bin at the same spatial scale. Our work also quantified the importance of having a healthy perennial-grass understory and perennial-grass patches in conjunction with sagebrush cover across large landscapes. Our work suggests that understory grass communities at landscape scales may be limiting grouse occurrence in certain parts of Oregon. © 2021 The Authors. *Wildlife Society Bulletin* published by Wiley Periodicals LLC on behalf of The Wildlife Society.

KEY WORDS Conifer encroachment, cheat grass, greater sage-grouse, landscape conservation, perennial bunch grass, resource selection function, sagebrush, Threat-based State and Transition Models.

Ecosystems across the world have been fundamentally altered by both contemporaneous and legacy impacts of humans, and the rate of ecosystem change has increased in recent decades (Millennium-Ecosystem-Assessment 2005). Mitigating the effects of change on wildlife species has been characterized by

Received: 23 July 2019; Accepted: 1 February 2021
Published: 3 August 2021

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policies designed to ameliorate specific threats (Boyd et al. 2014*a*). Such policies have been useful in staving off species declines when causative agents are tied to specific anthropogenic factors that can be easily regulated (Grier 1982). However, the same policies do not eliminate the need for active management of conservation-reliant plant and animal species (Scott et al. 2005, Scott et al. 2010), or species impacted by more complex problems associated with ecosystem dysfunction (Benson 2012). For such species, effective conservation is synonymous with adaptively managing persistent and complex threats (Boyd and Svejcar 2009) to the ecosystem processes that create and maintain functional habitat (Meretsky et al. 2000, Evans et al. 2013).

Sage-steppe vegetation in the northern Great Basin of the U.S. is being threatened by a variety of factors including direct conversion through anthropogenic development and habitat modifications (USFWS-DOI 2010) and indirect conversion as a secondary consequence of ecosystem dysfunction. Ecosystem dysfunction is being driven by both present day and legacy factors that exacerbate invasion of annual grasses and expansion of native conifer populations, primarily Western Juniper (*Juniperus occidentalis*), both of which are associated with altered fire regimes (Davies et al. 2011). Invasion of annual grasses and expansion of native conifer populations represent complex and persistent ecosystem threats that are not likely to be ameliorated using regulatory-based approaches alone, and instead require sustained conservation investment and an adaptive approach to management within a multi-stakeholder framework. For example, restoration of sagebrush habitat invaded by exotic annual grasses such as cheatgrass (*Bromus tectorum*) is a two-part process involving minimizing the abundance of unwanted annuals while restoring desired perennial vegetation. A variety of chemical and biologically-based options are available for reducing annual grass abundance (Davies et al. 2014). However, the appropriate techniques and practices for restoration of desired perennials vary in both space and time in accordance with a multitude of biotic and abiotic factors such that appropriate management depends on both seasonal timing and ecological location (Boyd and Svejcar 2009).

Disconnect between complex ecosystem problems and contemporary land-management policy and decision-making is highlighted by the challenges inherent in conservation of greater sage-grouse (*Centrocercus urophasianus,* hereafter sage-grouse). Populations of sage-grouse are declining in association with both species-specific, as well as ecosystem-based, problems such as conifer and annual grass invasion (Knick and Connelly 2011). Policy and regulations can be effective for species-specific issues such as energy development (Walker et al. 2007), but it would be impractical to attempt to regulate exotic annual grass similarly (Boyd et al. 2014*a*). Estimates suggest that habitat invasion by exotic annual grasses and-or expansion of native conifer populations is a widespread threat to 33 of 39 major sage-grouse populations (USFWS-DOI 2013). Addressing these issues is complicated by the fact that there is a growing diversity of societal values and expectations being placed on natural resources that lead to differing expectations and definitions of management success.

Improving communication and building trust through participatory decision making can lead to better conservation outcomes and social acceptance of conservation decisions (Addison et al. 2013). Key to participatory process is the development of a shared vision (Biggs et al. 2011). Creating threat-associated, mental ecological models with a diverse set of stakeholders can facilitate the creation of shared vision, because mental models translate complex ecological information into tangible and implementable conservation projects (Biggs et al. 2011). To facilitate large-scale adoption of conservation practices on private lands in Oregon, researchers, agency employees, and landowners developed mental models that focused on two pervasive threats to the sagebrush ecosystem: invasive annual grasses and conifer encroachment (Johnson et al. 2019). The process used State and Transition Models (STM) to classify variation in current plant community composition and structure (states) and described associated factors that drive plant community transitions from one state to another (Westoby et al. 1989). Over a 6-year period, the group developed Threat-based State and Transition Models (TBSTM), which simplified existing STMs with the intent of facilitating stakeholder communication and conservation delivery. The TBSTM framework adopted the original approach proposed by Westoby et al. (1989) in which only major vegetation states were identified. The simple TBSTM models allowed stakeholders to focus effort on the most ecologically important threats to sage-grouse habitat in the Northern Great Basin, improve communication, build stakeholder agreement, and empower decision-making at large spatial scales. Because ecological states within models could be mapped at large spatial scales, they were widely adopted and are currently being used to inform rangeland management planning on over 1.5 million ha of public and private sagebrush rangeland in eastern Oregon.

Although ecological constructs supporting TBSTMs are generally well understood, the mental model framework is more relevant if it is quantitatively related to prominent management and policy challenges, such as allocating conservation effort in sage-grouse habitat. The TBSTMs were not initially empirically validated in relation to target metrics such as sage-grouse habitat selection. Given the wide adoption of these models by management agencies and conservation providers to improve sage-grouse habitat, it has become essential to understand whether these models accurately reflect the occurrence of sage-grouse on the landscape.

The objective of our study was to determine the quantitative linkage between sage-grouse habitat selection and the TBSTM framework. We developed spatially-predictive models using both traditional landcover variables, such as percent sagebrush within a 560-m or 6440-m buffer, and models that placed the TBSTM into landscape level ecologically-based bins, such as the percent State A (i.e., sagebrush cover with a perennial grass understory; Fig. 1, Table 1) within the same spatial scales. We evaluated if the ecologically based landcover classification bins from the TBSTM mental model could spatially predict locations of sage-grouse breeding areas equivalent to traditional landcover variables that have been studied for over a decade.

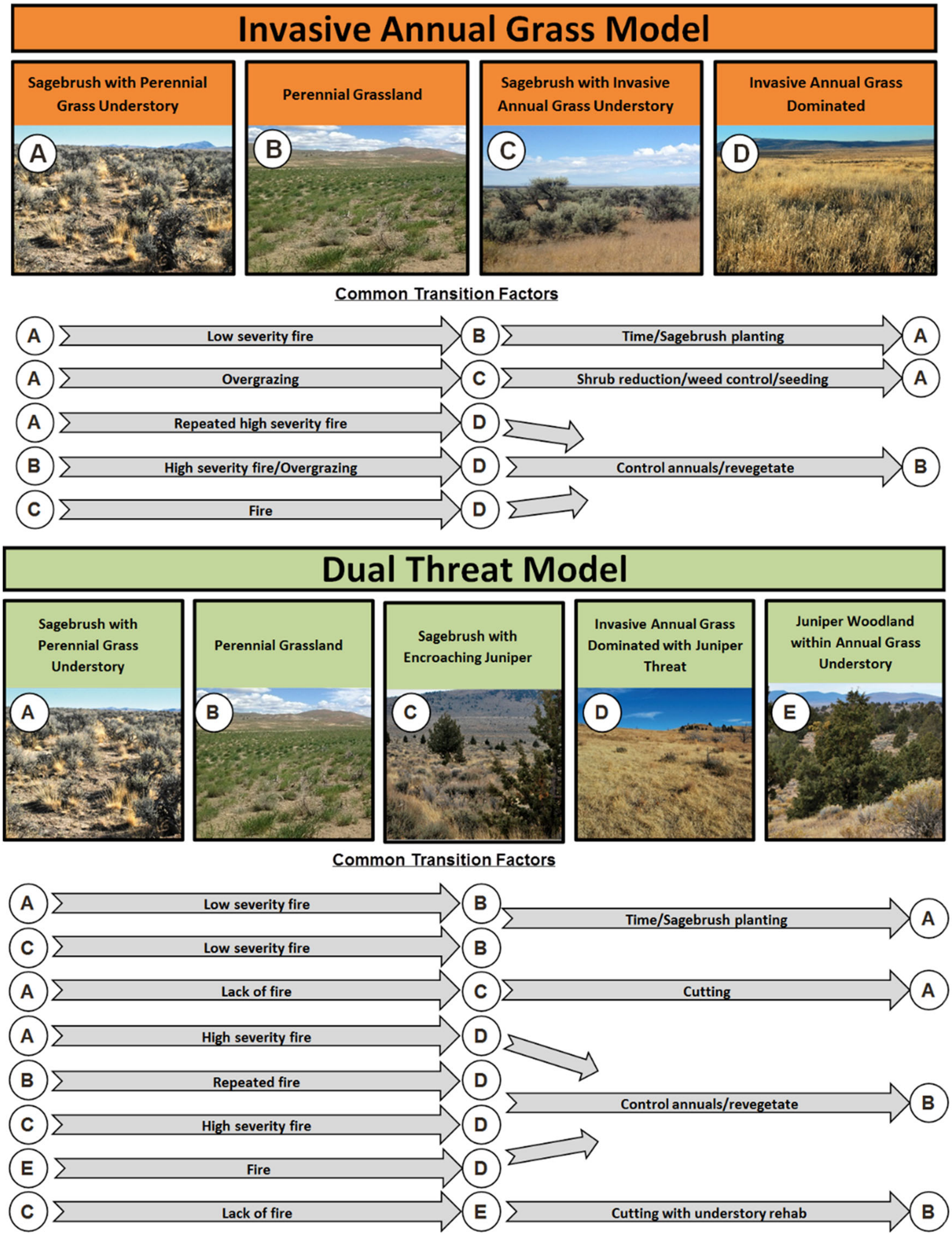

Figure 1. Conceptual ecological framework for managing sage-grouse habitat using generalized Threat-based state-and-transition models for sagebrush habitats threatened by annual grasses (top model) and by both annual grasses and expanding conifers (bottom model) in southeast Oregon, USA. States represent generalized categories of habitat structure and composition that are broadly representative of the variation in areas threatened by invasive annual grasses, or invasive annual grasses and conifers (Fuller et al. 2018, Johnson et al. 2019). Transition factors depict management and non-management factors that move habitat structure and composition between states.

STUDY AREA

Our study incorporated data collected between March 2013 and June 2017 in portions of 6 Oregon counties: Union, Baker, Grant, Malheur, Harney, and Lake. Within that broader geography, we specifically investigated 8 sage-grouse priority areas for conservation (PACs): 4 within the Snake River Plain Management Zone (Baker, Cow Valley, Bully Creek and Drewsey PACs) and 4 within the Northern Great Basin

Table 1. Description of Threat-based State and Transition Model (TBSTM) predictor variables used to predict sage-grouse occurrence in eastern Oregon, USA, 2013–2017. Names depict habitat States within TBSTMs that represent threats from either invasive annual grasses alone or both invasive annual grasses and conifers. All variables were resampled to a 30-m pixel and then the percent of the variable was calculated at 560-m and 6440-m radiuses.

Biotic variables					
Name of variable	**Variable abbreviations**	**Source (yr)**	**Native resolution**	**Description**	**Justification and reference**
TBSTM State A (all threats)	A	Fuller et al. (2018)	30 m	Sagebrush dominated with a perennial grass and forb understory.	We expected sage-grouse occupancy to be correlated positively with the abundance of Class A, because sage-grouse persistence is linked to conserving large blocks of sagebrush in good ecological condition (Knick and Connelly 2011, Knick et al. 2013).
TBSTM State B (all threats)	B	Fuller et al. (2018)	30 m	Perennial herbaceous dominated community.	We expected that sage-grouse occupancy would be correlated negatively to Class B because there is an established negative relationship between sage-grouse abundance and grasslands. (Patterson 1952, Aldridge et al. 2012).
TBSTM State C (annual grass threat)	C	Fuller et al. (2018)	30 m	Sagebrush dominated with annual dominated understory, usually invasive annual grasses.	Because of the inverse correlation between invasive annual grass abundance and perennial grass (Chambers et al. 2007, Davies 2008, Boyd and Svejcar 2011) and perennial forb abundance (Chambers et al. 2007), we expected that sage-grouse occupancy would correlate negatively with Class C.
TBSTM State D (annual grass threat)	D	Fuller et al. (2018)	30 m	Community dominated by annual vegetation, usually invasive annual grasses.	We expected sage-grouse occupancy to correlate negatively with Class D because lek trends decrease as exotic species increase (Coates et al. 2016).
TBSTM State C, D, E (conifer threat)	Con	Fuller et al. (2018)	30 m	Primarily juniper dominated with a full spectrum of understory conditions, from sagebrush dominated to annual and/or perennial grass dominated.	We expected sage-grouse occupancy to correlate negatively with Class C, D, and E because of the established negative relationship between sage-grouse and conifers (Doherty et al. 2008, Baruch-Mordo et al. 2013).
Non-Habitat	NonHab	Fuller et al. (2018)	30 m	Represent landscapes which are known non sage-grouse habitat.	Non-Habitat represents areas that are clearly not sage-grouse habitat including 1) NRCS Ecological sites that neither support sagebrush nor associated plant communities, 2) agriculture including residential or other infrastructure, and water bodies (Fuller et al. 2018).

Management Zone (Dry Valley-Jack Mountain, Steens, Beatys and Pueblo-S. Steens PACs; Fig. 2). The total study area size was 7,202,928 hectares (~17.8 million acres) and the area mapped within PACs with a 5-km buffer was 2,628,016 hectares (~6.5 million acres; Fig. 2). The study area encompassed the full latitudinal gradient in vegetative type present in Oregon, as well as important differences in the degree of primary threats to sage-grouse. For example, the Baker PAC (Fig. 2) was the northernmost PAC in the study area and lek counts had declined 75% from 2003 to 2017 (Bureau of Land Management, unpublished data). Primary threats to the Baker PAC were invasive weeds and conifer encroachment. In contrast, the Beaty's PAC was the largest PAC within Oregon and contained the most robust sage-grouse population in the state with a slightly increasing trend (L. Foster, Oregon Department of Fish and Wildlife, unpublished data). The Beaty's PAC was among the least fragmented and largest sagebrush-dominated landscapes within the extant range of sage-grouse (Knick and Hanser 2011).

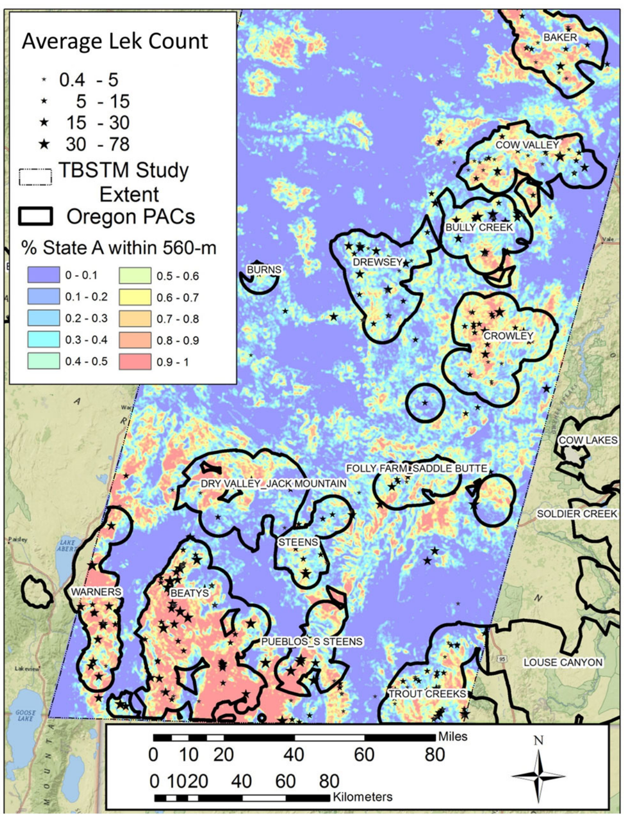

Figure 2. Spatial representation of the Threat-based State and Transition (TBSTM) framework in eastern Oregon, USA, during 2017. The TBSTM is a coarse representation of 9 sage-steppe vegetation states (ecologically-based bins) derived by simplifying desired sagebrush community characteristics and their primary ecological threats. The map shows the spatial location of State A habitats across Sage-grouse Priority Area of Conservation (PACs) in eastern Oregon, USA, in 2017. State A habitat represents sagebrush-dominated landscapes with perennial grass and forb understories. Lek data represent the average lek counts between 2013 and 2017.

METHODS

We quantitatively linked sage-grouse lek occurrence to a landscape level habitat classification based upon the TBSTM framework. We investigated whether TBSTM variables were able to spatially predict locations of sage-grouse breeding areas equivalently to landcover variables that have been studied for over a decade. We built spatially-predictive models using both landcover variables, such as percent sagebrush within a 560-m or 6440-m buffer, and variables which quantified the amount of TBSTM landscape level habitat classes (e.g., amount of State A within the same spatial scales).

Response Data

We used lek locations as a surrogate for nesting and early brood-rearing habitat because persistent lek formation is unlikely to occur in landscapes that do not support recruitment through time. Numerous publications have shown lek locations to be good predictors of important breeding areas for sage-grouse at landscape scales (Holloran and Anderson 2005, Doherty et al. 2010, Doherty et al. 2011, Coates et al. 2013, Fedy et al. 2014). In this regard, we are modeling lek locations as a surrogate to represent the landscapes that support successful nesting and early brood-rearing habitat critical to recruitment and maintenance of sage-grouse populations. Nesting females exhibit strong site fidelity with much longer distances between interannual nest sites for unsuccessful nesters vs. successful nesters (e.g., average distances 5.2 km vs. 1.6 km [Schroeder and Robb 2003], 0.5 km vs. 0.3 km [Holloran and Anderson 2005]). Through time, nest site fidelity promotes selection for less-risky habitats as sage-grouse slowly move away from areas that do not support recruitment (Holloran et al. 2010).

We used locations of active sage-grouse leks ($n = 311$) during 2013–2017 and pseudo-absence points ($n = 622$) to quantify the biological link between sage-grouse occurrence, traditional landcover variables, and TBSTM habitat classification. A lek was defined as active for analyses if there were ≥2 males counted during the most recent survey between 2013 and 2017. There have been extensive efforts in Oregon to identify sage-grouse lek locations over the last decade including both aerial and ground-based survey efforts (Foster 2017). Although it is likely some unidentified leks exist, we are confident that the spatial processes governing lek locations were well represented in the data (Foster 2017).

Predictor Data

Variable descriptions.—We distilled the sage-grouse habitat selection literature behind the traditional landcover model and the TBSTM model (Tables 1–3). We included descriptions of why variables were tested and the primary literature that supports inclusion. The tables include both variables that have been used in traditional landcover models and variables that put the TBSTM framework into a landscape context as well as abiotic variables used in both analyses. Transition factors that move habitats between states are not a specific focus of the current effort but are documented in the literature (Davies et al. 2011, Boyd et al. 2014*a*, Johnson et al. 2019).

Table 2. Description of abiotic variables used to predict sage-grouse occurrence in eastern Oregon USA, 2013–2017. Abiotic variables were held constant between the model developed with Threat-based State and Transition Model (TBSTM) class variables and those derived with habitat variables that have been traditionally used to predict sage-grouse locations. All variables were resampled to a 30-m pixel and then the percent of the variable was calculated at 560-m and 6440-m radiuses.

Abiotic variables—held constant under both analysis					
Name of variable	**Variable abbreviations**	**Source (yr)**	**Native resolution**	**Description**	**Justification and reference**
Terrain Ruggedness Index (TRI)	tri1	Riley (1999)	1000 m	Standard Deviation of elevation within 1000 m	Established negative relationship between sage-grouse and rough-terrain (Doherty et al. 2008, Fedy et al. 2014).
Multiscale Topographic Position (TPI)	tpi	Theobald et al. (2015)	270 m, 810 m and 2430 m	Multi-scale index of the location of grid cell (ex. Upper slope and warm vs. lower slope and cool)	Intermediate scale driver of ecological processes that can drive site scale invasion of localized habitat (Theobald et al. 2015).
Elevation	el	National Elevation Data (2013)	10 m	Average elevation within a buffer of the grid cell	Driver Ecological Processes and spatial auto correlation.
Normalized Difference Vegetation Index	NDVI	User Generated from Landsat-7 imagery	6400 m	Index to the amount of green living vegetation	Forbs are important predictors of early brood survival and habitat selection (Crawford et al. 2004).
Palmer Drought Severity Index	PDSI	Abatzoglou et al. (2017)	$2.5^\circ \times 2.5^\circ$	Estimate of relative dryness on a −10 (dry) to a +10(wet) scale	Large-scale ecological driver of land types. Hypothesized regional scale relationship between sagebrush landscapes with higher production. Documented carry over effects (Guttery et al. 2013, Blomberg et al. 2014).
Spring Precipitation	s.prcp	Thornton et al. (2012)	1000 m	Precipitation from March 15th–July 15th	Large-scale ecological driver of land types. Hypothesized regional scale relationship between sagebrush landscapes with higher production. Documented carry over effects (Blomberg et al. 2013, Blomberg et al. 2014).
Winter Precipitation	w.prcp	Thornton et al. (2012)	1000 m	Precipitation from Dec 1–Mar 14	Large-scale ecological driver of land types. Hypothesized regional scale relationship between sagebrush landscapes with higher production. Documented carry over effects (Blomberg et al. 2013, Blomberg et al. 2014).
Maximum Temperature	tmax	Thornton et al. (2012)	1000 m	Average Max Temp	Large-scale ecological driver of land types.
Minimum Temperature	tmin	Thornton et al. (2012)	1000 m	Average Min Temp	Large-scale ecological driver of land types.

Table 3. Description of traditional biotic landcover classification variables used to predict sage-grouse occurrence in eastern Oregon USA, 2013–2017. All variables were resampled to a 30-m pixel and then the percent of the variable was calculated at 560-m and 6440-m radiuses.

Name of variable	Variable abbreviations	Source (yr)	Native resolution	Description	Justification and reference
				Traditional biotic variables	
Sagebrush	Sage	LANDFIRE EVT 1.4.0 (2014)	30 m	Proportion of grid cells classified as sagebrush.	Established positive relationship between sage-grouse abundance and sagebrush (Patterson 1952).
Cropland	Crop	LANDFIRE EVT 1.4.0 (2014)	30 m	Proportion of grid cells classified as cropland.	Established negative relationship between sage-grouse and cropland (Knick et al. 2013, Fedy et al. 2014).
Developed	Dev	LANDFIRE EVT 1.4.0 (2014)	30 m	Proportion of grid cells classified as developed.	Established negative relationship between sage-grouse abundance and developed (Knick et al. 2013).
Grassland/ Herbaceous	Grass	LANDFIRE EVT 1.4.0 (2014)	30 m	Proportion of grid cells classified as annual or perennial grassland/herbaceous.	Established negative relationship between sage-grouse abundance and grasslands (Patterson 1952).
Pinyon Juniper	PJ	LANDFIRE EVT 1.4.0 (2014)	30 m	Proportion of grid cells classified as Pinyon/Juniper.	Established negative relationship between sage-grouse and conifers (Doherty et al. 2008, Baruch-Mordo et al. 2013)
Woodland	WD	LANDFIRE EVT 1.4.0 (2014)	30 m	Proportion of grid cells classified as woodlands other than pinyon/juniper and riparian woodland classifications.	Established negative relationship between sage-grouse and conifers (Doherty et al. 2008, Baruch-Mordo et al. 2013).
Woodland/ Riparian	W.rip	LANDFIRE EVT 1.4.0 (2014)	30 m	Proportion of grid cells classified as riparian woodlands.	Established negative relationship between sage-grouse and conifers (Doherty et al. 2008, Baruch-Mordo et al. 2013).

The TBSTM framework is a coarse representation of 9 sage-steppe vegetation states (ecologically-based bins) derived by simplifying desired sagebrush community characteristics and their primary ecological threats in Oregon (Fig. 1). In our case, threats are invasive annual grasses and expanding conifer populations and we built a separate model for each of these vegetation states. States vary on an A–E scale, with State A habitat as an expression of both a healthy sagebrush overstory, and perennial bunchgrass understory. State B habitat is perennial grassland lacking sagebrush cover. States C–E habitat are an increasing expression of either invasive annual grass, conifers, or both, with concomitant reduction in sagebrush and-or perennial grasses (Fig. 1). For the purposes of quantitatively linking the TBSTM to sage-grouse, we combined all conifer threat states into a single class because of known avoidance of conifer trees (Doherty et al. 2008, Baruch-Mordo et al. 2013, Fedy et al. 2014). However, for habitat treatment the TBSTM framework has 3 Threat-based conifer states, all of which correspond to different conifer management options (Johnson et al. 2019).

We developed a TBSTM habitat classification map (Fig. 2) across much of the sage-grouse range in Oregon using the published methods of Sant et al. (2014). The landcover mapping system of Sant et al. (2014) classifies each 30-m pixel in the landscape into 9 categories (Table 1) representing habitat states described by the TBSTM framework (Fig. 1). Thus, our TBSTM habitat classification map generalizes vegetation communities based on cover of sagebrush, native perennial bunchgrasses, conifers, and invasive annual grasses, and describes the factors which may cause community transition between these states (Johnson et al. 2019). Accuracies of the TBSTM map support landscape level modeling and ranged from 73% to 84% in mapped areas in PACs (E. Sant, US Fish and Wildlife Service, unpublished data).

Scale.—Past research has shown thresholds of habitat selection at multiple scales affect sage-grouse habitat use. We quantified how much state A habitat (i.e., sagebrush cover with a perennial grass understory) was needed to promote habitat selection by sage-grouse. We also wanted to quantify thresholds of threats as classified by the TBSTM that would preclude habitat use by sage-grouse (i.e., the percent of State C, D, and conifer within either 560 m or 6440 m, Table 1). We produced response curves for all variables retained in the final model to understand the scale(s) at which TBSTM habitat are selected and how occupancy changes with different percentages of TBSTM bins (Table 1) in the larger landscape. Variable response curves depict the relationship between habitat selection and each predictor variable in the final model. Variable response curves are produced by iterating through the entire observed range of a predictor variable while holding all other variables at their mean values (Young 2012). We included measures of precision for all relationships at various significance levels so practitioners could understand both the shape and precision of the habitat relationship. To understand the relative influence of each habitat predictor, we successively computed the change in AUC when each individual predictor was removed from the final model (Young 2012).

Variable Groupings.—We conducted a simple statistical test to see if a model that used the TBSTM framework to describe habitat (Fig. 1, Tables 1 and 2) could compete with other variables that have been used for over a decade to model sage-grouse habitat selection (Tables 2 and 3). Lek occurrence is influenced by patterns of vegetation, as well as heterogeneity in abiotic factors such as topography and climate (Doherty et al. 2010, Ricca et al. 2018). We created 2 potential suites of habitat predictor variables for sage-grouse and compiled them into a GIS database representing biotic (Tables 1 and 3) and abiotic variables of ecological relevance (Table 2). We characterized the percent of biotic and abiotic variables at 560 m and 6440 m distances from leks and pseudo-absence points because these distances are known to be important for breeding habitat selection for sage-grouse (Aldridge et al. 2012, Doherty et al. 2016, 2018). The first model suite consisted of TBSTM biotic habitat variables (Table 1). The second model suite consisted of traditional biotic variables derived from LANDFIRE 1.4.0 (LANDFIRE 2014) (Table 3). We held our suite of abiotic variables (Table 2) constant between models to allow a direct comparison of how well the TBSTM biotic habitat classes predicted lek occurrence compared to traditional biotic variables derived from LANDFIRE 1.4.0 (LANDFIRE 2014).

Statistical Modeling

We modeled the presence of active lek locations with a generalized linear model with a logit-link function throughout the spatial extent of the TBSTM habitat classification map (Fig. 2). We compared habitat characteristics surrounding active lek locations to habitat characteristics around random pseudo-absence locations constrained within a minimum convex polygon that contained all active lek locations. Our breeding habitat model provided the probability of each 30-m grid cell containing sufficient habitat to support an occupied lek.

We used the Software Assisted Habitat Modeling (SAHM) (Morisette et al. 2013) program developed by the U.S. Geological Survey to generate fit statistics between models developed with traditional landcover variables (Table 3) and those built using the TBSTM to represent biotic habitat components (Table 1). We specifically chose the SAHM modeling interface to R (R Core Team 2018), because the SAHM framework has been widely tested, is peer reviewed (Morisette et al. 2013), and research that used SAHM has been extensively published in a wide variety of journals (Luo et al. 2015, Evangelista et al. 2018, Jarnevich et al. 2018).

We used the standard model fitting procedure in SAHM for generalized linear models (Young 2012). The SAHM uses open-source R code to implement statistical models within program R (R Core Team 2018) through the SAHM interface (Morisette et al. 2013). We did not allow 2 variables to be in a candidate variable set if their univariate correlations were >0.7. Models were fit by first calculating an Akaike Information Criterion (AIC) score to a null model and all individual covariates in the model. We first added the variable that most improved AIC over the null model. We treated the resultant model as fixed and repeated the step with the additional variables. The model selection procedure was completed when there was no improvement in AIC with the addition or removal of variables (Young 2012). We allowed both quadratic functions and interactions between variables in our analyses as we knew *a priori* that sagebrush and perennial grass resilience to disturbances and resistance to invasive species occur within climatic envelopes and interact with other biotic factors (Chambers et al. 2017). Further, numerous publications have documented quadratic functional response curves to habitat selection of sage-grouse (Connelly et al. 2000, Hagen et al. 2007).

We compared 3 validation statistics between the traditional landcover and TBSTM models to understand model fit. We evaluated percent correctly classified, area under the curve (AUC), and coefficient of determination (R^2) to determine model fit. We felt modeling quadratic functions and interactions was biologically warranted, but also knew this could lead to an over-fit model. Therefore, we investigated relative loss in predictive power through k-fold cross-validation which consisted of 10% of lek and pseudo-absence locations. Our premise was simple: if we had high fit statistics when building the models, but low fit statistics when cross-validating our models, we would conclude our model was over fit to the data and we would build simpler models without interactions or quadratic functions.

RESULTS

Both the TBSTM and traditional landcover models exhibited good statistical fit (Table 4) and were largely comparable in their predictions of breeding areas for sage-grouse (Figs. 3 and 4). Model fit decreased slightly when we evaluated the k-fold cross-validation data set for both the TBSTM and traditional landcover models; however, fit statistics still showed a good model fit (Table 4). Our spatially explicit model generated from applying the final TBSTM and Tradition landcover models both predicted the locations of known active leks across our study area (Figs. 3 and 4).

Both models included 9 predictor variables with a quadratic effect of winter precipitation as the most important variable (Fig. 5, Table 2). Winter precipitation showed a strong climatic envelope with sage-grouse selecting for intermediate values (Figs. 6 and 7). The relative strength of winter precipitation was twice as strong in the traditional landcover model vs. the TBSTM model (Fig. 5). Variable importance for both sagebrush and State A as well as conifer were equivalent across models. Consistent with current

Table 4. Model fit statistics for the spatial prediction of sage-grouse breeding habitat using either the Threat-based State and Transition Model (TBSTM) or Traditional Landcover Model in eastern Oregon, USA, 2013–2017.

	Correlation coefficient	Area under the curve	% Correctly classified
TBSTM	0.70	0.91	83%
TBSTM Cross-Validation	0.64	0.88	79%
Tradition landcover model	0.65	0.89	80%
Tradition landcover model Cross-Validation	0.59	0.86	76%

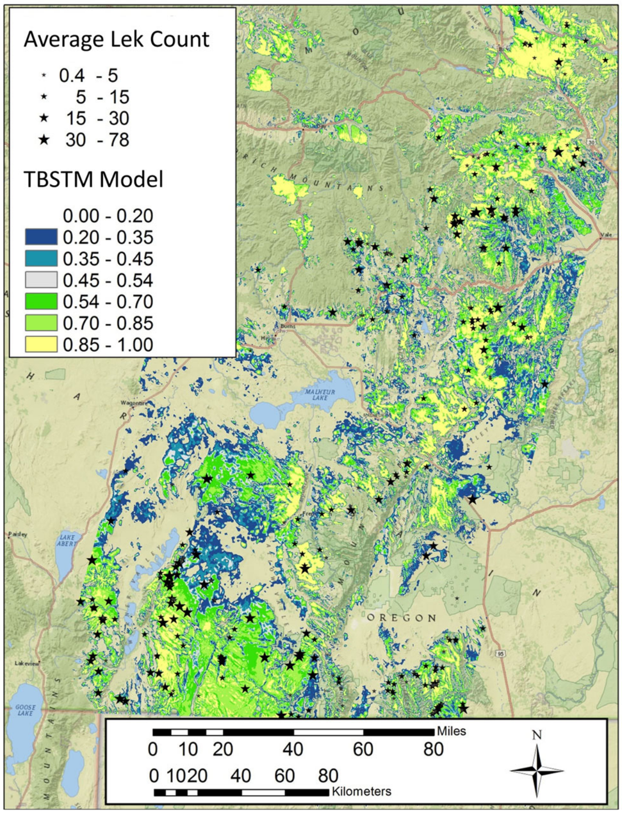

Figure 3. Spatial prediction of sage-grouse breeding habitat as defined by our Threat-based State and Transition Model in eastern Oregon, USA, 2013–2017. Our breeding habitat model provided the probability of each 30-m grid cell containing sufficient habitat to support an occupied lek. Probabilities between 0.00 and 0.20 are clear to allow spatial referencing of prediction location to local readers. Lek data represent the average lek counts between 2013 and 2017.

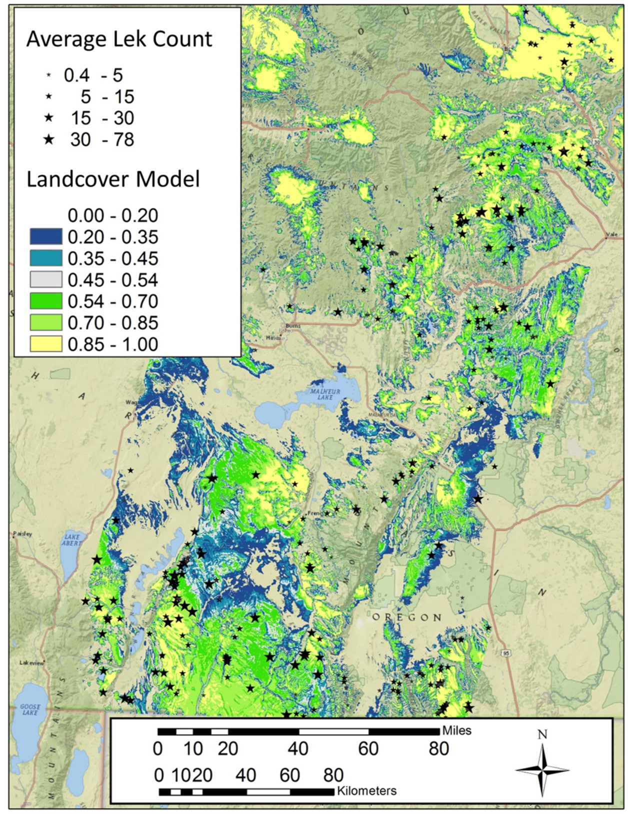

Figure 4. Spatial prediction of sage-grouse breeding habitat as defined by our traditional landcover model in eastern Oregon, USA, 2013–2017. Our breeding habitat model provided the probability of each 30-m grid cell containing sufficient habitat to support an occupied lek. Probabilities between 0.00 and 0.20 are clear to allow spatial referencing of prediction location to local readers. Lek data represent the average lek counts between 2013 and 2017.

knowledge, sage-grouse selected for relatively flat (Tri1 <26 TBSTM model, <37 traditional landcover model), sagebrush dominated landscapes (>48% Sagebrush 560, or >50% State A), with low tolerance for human disturbance (<4% Crop 6440 or <6% NonHab_560) and even lower tolerance for conifer encroachment (<3% PJ560 or <3% Con560; Figs. 6 and 7).

The 560-m scale was consistently the most important scale in the TBSTM model, whereas the traditional landcover model included a mix of 6440 m and 560 m in the final models (Figs. 6 and 7). Grass cover was an important variable in both models, however LANDFIRE (2014) does not differentiate between annual and perennial grass cover like TBSTM habitat classification does. We found selection for >8% perennial grass (State B) to be steep and asymptotic (Fig. 6). Annual grass (State D) was not included in the final model after model selection; however, it did show a negative relationship when tested in univariate space. LANDFIRE (2014) effectively combines State B (perennial grass dominated) and State D (annual grass dominated) habitats into a single habitat classification. The combined response of grass6440 was positive, but the strength of selection was not as steep compared to State B (Figs. 6 and 7). The TBSTM was also able to compare the effects of a sagebrush dominated cover with a perennial grass understory (State A) vs. a sagebrush dominated cover with an annual grass understory (State C). We show State C habitat exhibited higher variability in predicting grouse occurrence than most retained TBSTM variables ($p < 0.1$) and exhibited a flat selection function (0% State C probability = 50%, 100% State C probability = 52%; Fig. 6). State C habitat also showed a negative response when tested in univariate space.

DISCUSSION

We showed that our TBSTM model was equivalent to a traditional landcover model in calculating the location of sage-grouse breeding habitats. We quantified a direct biological link between the TBSTM framework and sage-grouse occupancy and tested its predictive ability against known methods that have been used widely for over two decades (Boyce and McDonald 1999). Having a quantitative link between the TBSTM and sage-grouse occupancy allows insight into the biological effectiveness of transitioning habitats between TBSTM states as well as understanding how much habitat needs to be treated within priority areas. Ultimately, having a quantitative link between the TBSTM and sage-grouse occupancy allows for scenario planning before

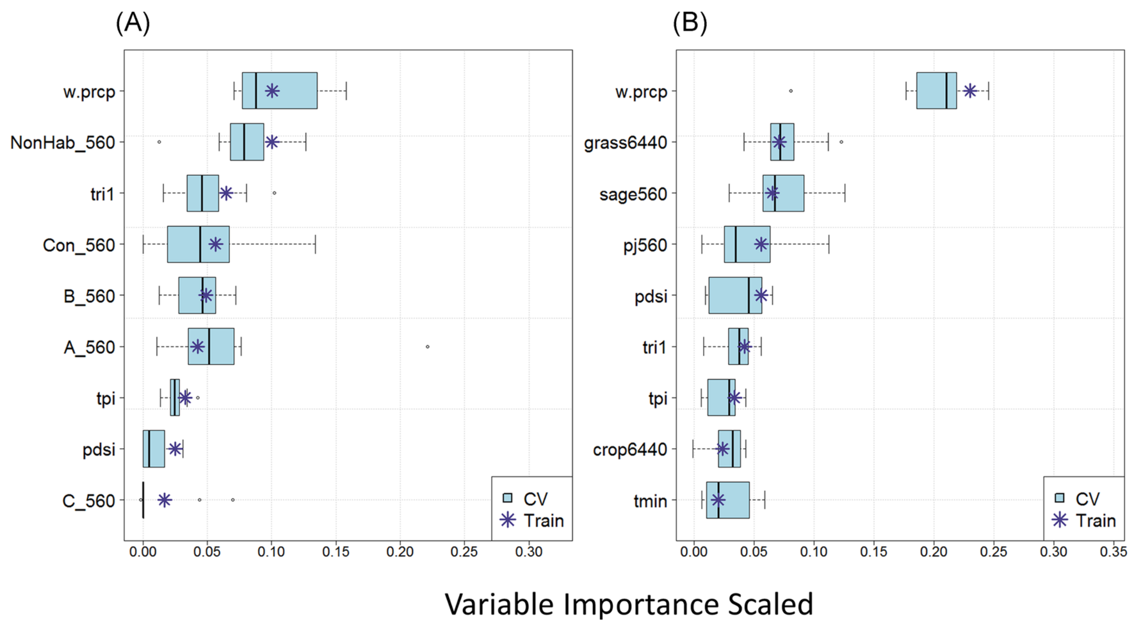

Figure 5. Variable importance as calculated by the change in area under the curve (AUC) when each predictor variable is systematically removed from the final model. Panel A represents the importance of each retained variable in the final Threat-based State and Transition Model (TBSTM) model. Panel B represents the importance of each retained variable in the final traditional landcover model. The _SCALE suffix represents the percent of each habitat bin within a 560-m or 6440-m buffer. For variables that were not resampled because of a high degree of spatial autocorrelation, the y-axis defines full range of the variables sampled by our response data. w.prcp, winter precipitation; NonHab, non-habitat; tri1, terrain roughness index; tpi, multiscale topographic position; pdsi, Palmer Drought Severity Index; tmin, average yearly minimum temp.

conservation actions are implemented at landscape scales (Doherty et al. 2018, Ricca et al. 2018).Consistent with past and present research, landscape context within the TBSTM framework is important to sage-grouse (Doherty et al. 2010, Ricca et al. 2018). We found strong positive selection for both State A habitat (healthy sagebrush-perennial bunchgrass communities), and State B habitat (perennial bunchgrass-dominated communities), but neutral selection for State C habitat (sagebrush with invasive annual grass, or fully depleted understories). At a landscape scale, State A habitat will not be occupied until roughly half of a 98.4 ha area is in State A habitat. Further, State A habitat must also have low amounts of threats such as non-habitat 560 (<6%) or conifer encroachment (<3%) within a 560 m buffer (i.e., 98.4 ha area; Fig. 6). We found little difference in response to conifer metrics between the TBSTM models and the traditional landcover models, with marked reduction in probability of selection when conifer exceeded approximately 3% of the landscape at the 560 m scale within both models. Our results are consistent with a growing body of research describing sage-grouse response to conifer encroachment (e.g., Baruch-Mordo et al. 2013, Coates et al. 2017).

The new information within our study (relative to extant sage-grouse literature) is the selection for perennial bunch grasses (State B) and the lack of selection for sagebrush with invasive annual grass, or fully depleted understories (State C, annual grass threat model; Fig. 1). Recent research showed the correlation between sage-grouse nest success and grass height was a product of a phenological bias in many study areas (Gibson et al. 2016, Smith et al. 2018, Smith et al. 2020). The phenological bias was unfortunately posited by some to indicate that grass does not matter for sage-grouse. We show healthy perennial bunchgrass communities are crucial to promoting sage-grouse habitat utilization at landscape scales (i.e., selection for States A and B). The importance of perennial grasses is also evident as an understory component within sagebrush stands when comparing habitat selection for State A (sagebrush with perennial bunch grass understory) vs. State C (Sagebrush with annual grass understory; Fig. 6). The disparity in selection for State A and State C habitat evident in our modeling suggests that not all sagebrush cover is created equal. Sage-grouse may not actively avoid areas impacted by invasive annual grasses when a mature sagebrush over story is present (State C); however, these systems are not actively selected in Oregon. Past work on nesting sage-grouse demonstrated avoidance of invasive annual grasses at an individual level within local scales (Kirol et al. 2012). Further, given the prevalence of annual grasses in State C habitat, these areas are susceptible to conversion to annual grass dominance (i.e. State D) following wildfire (Brooks et al. 2015). Invasive annual grass monocultures showed a negative relationship when tested in univariate space, but were not carried through in our modeling effort. However, previous research has demonstrated the negative impacts of invasive annual grass monocultures on sage-grouse population growth (Coates et al. 2016). New maps of invasive annual grass occurrence give insight into areas that may be predicted to be sage-grouse habitat, but are at risk of loss in the near future (Boyte and Wylie 2016, Jones et al. 2018, Rigge et al. 2019). Collectively, poor understory conditions

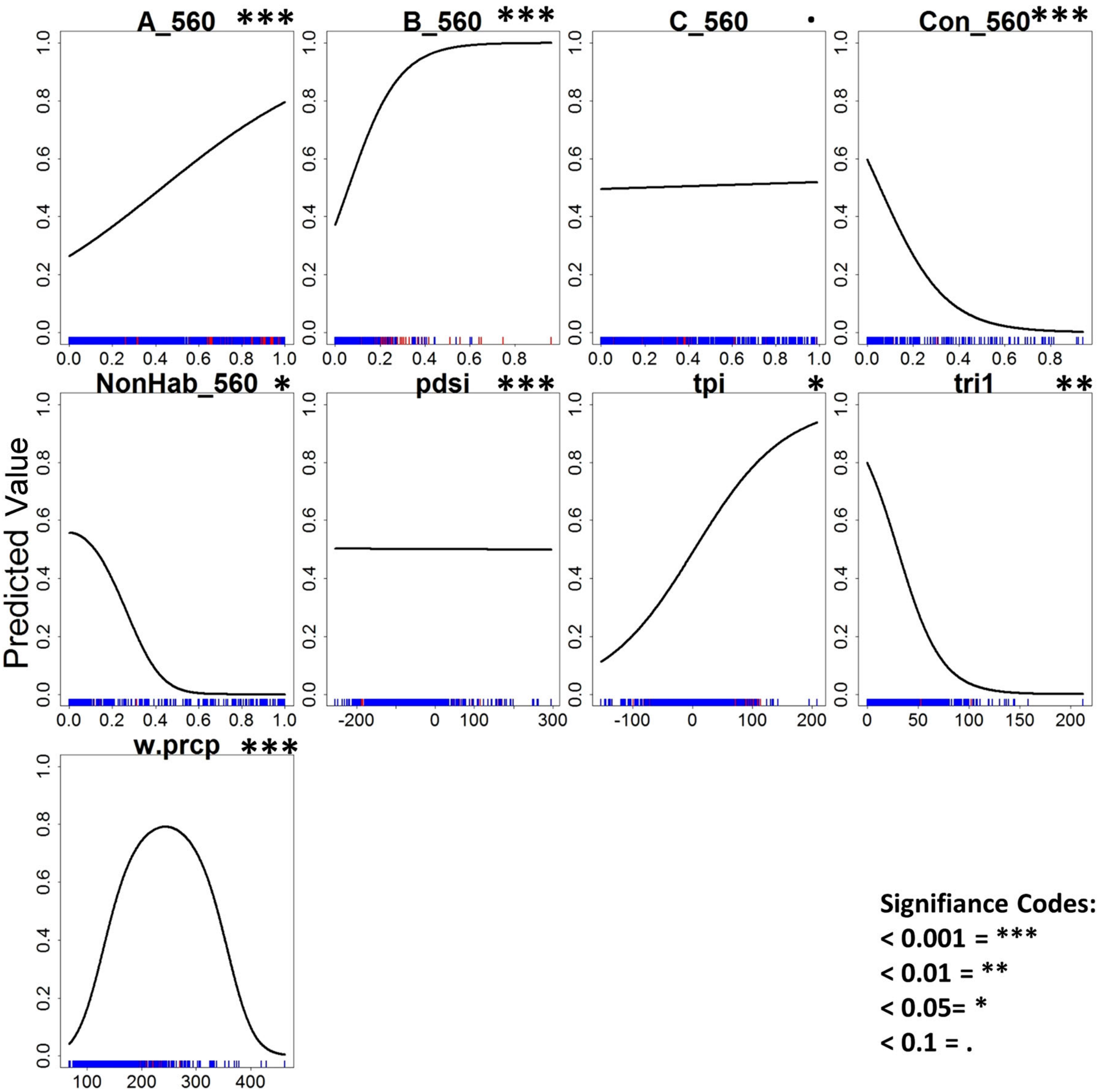

Figure 6. Habitat selection response curves for each variable within the final Threat-based State and Transition Model of sage-grouse occurrence in eastern Oregon, USA, 2013–2017. The y-axis represents the probability of containing sufficient habitat to support an occupied lek. The x-axis represents the percent of each habitat bin within a 560-m buffer. For variables that were not resampled because of a high degree of spatial autocorrelation, the x-axis defines full range of the variables sampled by our response data. w.prcp, winter precipitation; NonHab, non-habitat; tri1, terrain roughness index; tpi, multiscale topographic position; pdsi, Palmer Drought Severity Index.

at 560-m and 6440-m scales appear to have limited sage-grouse distributions across our study area, which is especially concerning given the lack of effective tools available to managers to address annual grass invasion currently.

Our analyses were a pilot effort and proved the concept of the TBSTM framework in predicting sage-grouse occurrence. Having a large pilot extent allowed insight into the relative importance of different PACs. However, having one global extent effectively averages out finer-scale spatial heterogeneity within localized areas, resulting in a more generalized model (Boyce 2006). Aligning the scale of habitat models with the scale of resource management can increase the utility of the models for management decisions (Hobbs 2003). Aligning scales is important because a generalized model could fit well for the larger study area, but not predict well for certain localized areas. The spatial predictions in the furthest northeast area (Baker PAC) were not consistent with local knowledge of the area and the threats identified within the TBSTM habitat classifications. Difference in threats by PAC in Oregon indicated that we may need to investigate smaller extents for certain PACs or regional grouping of PACs within a Management Zone (Stiver et al. 2006). Further, we believe validation of results with sage-grouse telemetry data in addition to the validation of TBSTM models with our hold-out test data set is prudent. Regardless, the model fit statistics of our pilot effort were good and clearly show the utility of the TBSTM framework.

Addressing key ecological threats to persistence of sage-grouse and the sagebrush habitat they depend on requires engagement and investment by a diversity of stakeholders, the majority of whom are not professional plant ecologists,

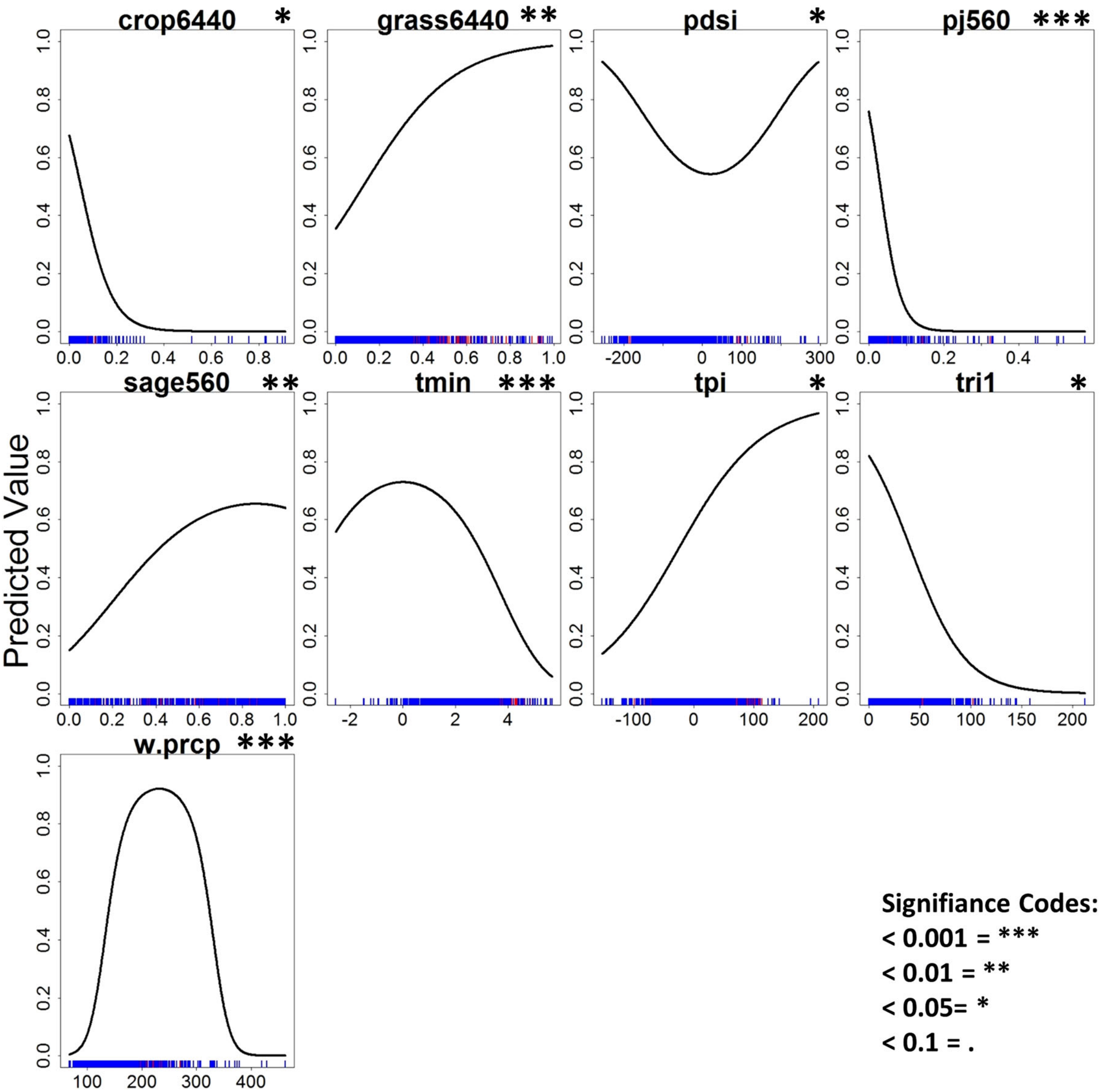

Figure 7. Habitat selection response curves for each variable within the final Traditional Landcover model of sage-grouse occurrence in eastern Oregon, USA, 2013–2017. The y-axis represents the probability of containing sufficient habitat to support an occupied lek. The x-axis represents the percent of each landcover class within a 560-m or 6440-m buffer. For variables that were not resampled because of a high degree of spatial autocorrelation, the x-axis defines full range of the variables sampled by our response data. w.prcp, winter precipitation; tri1, terrain roughness index; tpi, multiscale topographic position; pdsi, Palmer Drought Severity Index; tmin, average yearly minimum temp.

wildlife biologists, or land managers. State and Transition Models provide a highly visual tool that can, in theory, be used to engage such an audience. However, STMs are often designed to convey a complexity of information that is not appropriate for the more generalized understanding of a diversity of end-users. To that end, the value of our simplified TBSTM framework was initially recognized through its use as an effective communication tool among conservation stakeholders (Boyd et al. 2014*b*). The TBSTM framework was used to assess habitat attributes on private land, communicate that information with landowners and other entities, and to help determine management direction. Participants included plant ecologists, wildlife biologists, ranchers, elected officials, business interests, science advisors, and sportsmen (USFWS-DOI 2014). The mutual understanding developed within the TBSTM process allowed for the development of sage-grouse Candidate Conservation Agreements with Assurances in Oregon between the USFWS and 5 local soil and water conservation districts who work to enroll interested landowners. Candidate Conservation Agreements with Assurances are voluntary conservation agreements between non-federal landowners and the Service, wherein enrolled landowners implement conservation measures to address threats to candidate species. In return the Service provides assurance to the landowner that no additional actions will be needed on enrolled lands, as well as incidental take coverage for covered activities on enrolled lands should the species be listed in the future. The TBSTM framework has also been adapted to form the backbone of the State of Oregon's Sage-Grouse Habitat Quantification Tool for assessing development impacts to habitat, and is being piloted by BLM to rapidly assess and prioritize ecological threats from annual grasses and conifer encroachment in grazing allotments. The success of these programs suggests that simple mental models, like the TBSTMs, are effective aids to conservation planning, which is consistent with expectations (Biggs et al. 2011, Tulloch et al. 2015).

MANAGEMENT IMPLICATIONS

The benefit of a spatially explicit mental model is that it helps promote communication among stakeholders, while predicting where threats to sage-grouse breeding habitat are occurring and simultaneously highlighting how each threat could be treated to transition habitats to State A. This type of linkage between spatial orientation of threats and structured decision-making has been recognized as an effective means to advance conservation outcomes. Given finite resources for conservation investment, relative to the scale of the primary ecological challenges, cost-effective deployment of resources will be critical for sage-grouse and sagebrush steppe conservation. Additionally, our TBSTM framework includes management associated (e.g., grazing modification) and ecosystem process (e.g., wildfire) transition factors that have the potential to move habitat from current to desired states. These transition factors allow managers to develop management alternatives to both promote desired changes and manage against undesired changes. From a conservation planning standpoint, quantitatively linking the TBSTM framework to sage-grouse allows us to not only spatially prioritize and define specific habitat treatments in breeding habitat, but also to understand how expected biological outcomes for sage-grouse differ between different conservation investment strategies.

ACKNOWLEDGMENTS

We would like to thank Drs. E. Hamerlynck and K. Davies for reviews of an earlier draft of the manuscript. We would also like to thank M. Guttery (Associate Editor), A. Knipps (Editorial Assistant), J. Levengood (Editorial Assistant) and 3 anonymous reviewers for thoughtful comments that greatly improved the clarity of our presentation. Mention of a proprietary product does not constitute a guarantee or warranty of the product by the USDA or the authors and does not imply its approval to the exclusion of other products that may also be suitable. USDA is an equal opportunity provider and employer. Findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

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Associate Editor: M. Guttery.