Climate-change impacts on sagebrush habitat and West Nile virus transmission risk and conservation implications for greater sage-grouse

Anne Schrag · Sarah Konrad · Scott Miller · Brett Walker · Steve Forrest

Abstract Greater sage-grouse (*Centrocercus urophasianus*) are threatened by loss of sagebrush habitat and the spread of West Nile virus throughout much of their range in North America; yet, future impacts of climate change on these potential stressors have not been addressed. Here, we aim to quantify the potential impacts of climate change on the distribution of climatically suitable habitat for sagebrush and on transmission risk for West Nile virus in the eastern portion of the species' range. We used Maxent to model the current and future climatically suitable habitat for two dominant sagebrush species in the study area, and we used a degree-day model to predict future West Nile virus transmission risk under likely climate-change scenarios. Our models suggest that areas with the highest future suitability for sagebrush habitat will be found in southwestern Wyoming and north-central Montana. The degree-day model suggests that greater sage-grouse in western portions of the study area, which are generally higher in elevation than where West Nile virus currently occurs, will see increasing risk of transmission in the future. We developed a spatially explicit map of suggested management actions based on our predictions that will aid in conservation of the species into the coming decades.

Keywords Climate · Greater sage-grouse · Northern Great Plains · Northern Rockies · Species distribution modeling · West Nile virus

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Introduction

Successful conservation of species requires spatially explicit information on current and future threats to their survival (Margules and Pressey 2000). For species that encompass large geographical ranges, it is often necessary to apply a regional-scale approach to conservation, as opposed to working only locally or within jurisdictional boundaries (Ferrier et al. 2004). The sagebrush ecosystem, which spans the western US and Canada, is a system of high

conservation value that contains many species of conservation interest (Knick et al. 2003). However, anthropogenic and ecological changes threaten both sagebrush communities and sagebrush-dependent species (Knick et al. 2003; Connelly et al. 2004; Aldridge et al. 2008; Meinke et al. 2008).

One sagebrush-obligate species of heightened concern is the greater sage-grouse (*Centrocercus urophasianus*). The greater sage-grouse is no longer present along the periphery of its former range in North America (Schroeder et al. 2004), and long-term monitoring efforts suggest that populations throughout the West have declined over the past 40 years (Knick et al. 2003; Connelly et al. 2004; Aldridge et al. 2008). Studies have shown that decreases in the amount of sagebrush habitat lead to declines in sage-grouse abundance and declines have largely been attributed to loss and/or degradation of sagebrush habitat (Knick et al. 2003; Connelly et al. 2004; Aldridge et al. 2008; Meinke et al. 2008). More recently, impacts from infectious diseases such as West Nile virus (WNv) (Naugle et al. 2004, 2005; Walker et al. 2007a; Walker and Naugle 2010) and increasing habitat loss and degradation associated with energy development (Manville 2004; Walker et al. 2007b; Doherty et al. 2008; Naugle et al. 2010) have emerged as concerns.

Climate change is likely to influence sage-grouse conservation both directly and indirectly and may act synergistically with other stressors. Historically, sagebrush has inhabited cold, dry areas where it can outcompete shallow-rooted grasses and forbs (Wells 1970). Increasing temperatures and greater available moisture, especially later in the summer, may decrease its competitive advantage over these species (Schwinning et al. 2005). Increasing temperatures associated with climate change also may lead to earlier onset of WNv transmission and facilitate spread of the virus to higher elevations (Naugle et al. 2005). During periods of drought, which are expected to be more frequent and possibly more intense under climate change, sage-grouse may also move toward water earlier in the year and, subsequently, come into contact with mosquitoes for longer periods during the transmission season (Naugle et al. 2004). In addition, drought and severe winters have been found to decrease survival of greater sage-grouse broods and adults, respectively (Holloran et al. 2005; Moynahan et al. 2006; Aldridge and Boyce 2008). Climate

change may also lead to more frequent fires, which will yield a competitive advantage for grass species (Westerling et al. 2006). Invasive species, such as cheatgrass (*Bromus tectorum*), can cause fires to burn more frequently, which leads to a competitive disadvantage for fire-intolerant sagebrush species such as Wyoming big sagebrush (*Artemisia tridentata* var. *wyomingensis*; Baker 2006). Also, because many crops at northern latitudes are currently temperature-limited, warmer seasonal temperatures associated with climate change may lead to greater conversion of native shrub-steppe to tilled agriculture in the near-term (Motha and Baier 2005; Stubbs 2007).

Species distribution models can be used to quantify the relationship between the location of a species across the landscape and the climatic conditions that are suitable for their long-term viability (Pearson and Dawson 2003; Guisan and Thuiller 2005; Pearson et al. 2007). These models allow for examination of the predicted impacts of future climate change by replacing current climatic parameters with future predicted climatic variables, allowing for a comparison of the current and future climatically suitable habitat (e.g., Bradley 2009; Schrag et al. 2008). Some studies have argued that the practical application of species distribution models for making conservation decisions is limited because non-climatic factors, which are not taken into account in these models, also influence the distribution of species across the landscape (Pearson and Dawson 2003; Guisan and Thuiller 2005; Beale et al. 2008). However, other studies have shown that the basic principles that drive bioclimatic envelope modeling are supported, and the biogeographical information that these models provide can be useful in understanding which factors most highly influence spatial patterns of species across the landscape and how those patterns may change under future conditions (Martínez-Meyer et al. 2004; Pearson et al. 2007).

The goal of this paper is to inform current greater sage-grouse conservation actions by modeling potential impacts of climate change on two species of sagebrush and on the risk of West Nile virus transmission in the northern portion of their range. We chose this focal area because it lies at the periphery of their range in the US, and the impacts of climate on these species of sagebrush has not been examined at this scale. We first examined the impacts of climate change on the climatically suitable habitat

for two dominant sagebrush species in the eastern half of the species' range, Wyoming big sagebrush and silver sagebrush (*Artemisia cana*), using future predicted climate data from downscaled global circulation models (GCMs). Then, we examined the impact of climate change on the risk of West Nile virus transmission using degree-day models. When viewed in relation to the current known distributions of greater sage-grouse habitat, these analyses allowed us to make recommendations for conserving specific areas likely to provide high-quality sagebrush habitat in the future, as well as to identify areas where risk of West Nile virus transmission will increase.

Methods

Study area

The focal region for this study included the US states of Montana, Wyoming, North Dakota and South Dakota. The study area ranges in elevation from approximately 300 m in the eastern half of the Dakotas to over 4,000 m in the western parts of Wyoming. Eastern areas of the study region generally have higher overall temperatures, and western parts of the area show more temperature variability due to greater topographic relief. Precipitation falls primarily in the form of snow in mountainous portions of the study region, while most precipitation in the plains is rainfall.

Sagebrush distribution modeling: species data

Two species of sagebrush are common in the study area: Wyoming big sagebrush and silver sagebrush. We used point data from the LANDFIRE Program to map the distribution of these sagebrush species across the landscape (LANDFIRE 2009). The LANDFIRE Program compiles digital maps of vegetation composition throughout the U.S. Numerous surveys—all with distinct objectives—are used to sample and classify vegetation on the ground. LANDFIRE personnel assisted us by developing a database that included the Global Positioning System coordinates of each presence point location for the two species of sagebrush (Fig. 1). We used a total of 973 points for silver sagebrush and 1,160 points for Wyoming big sagebrush for the analysis.
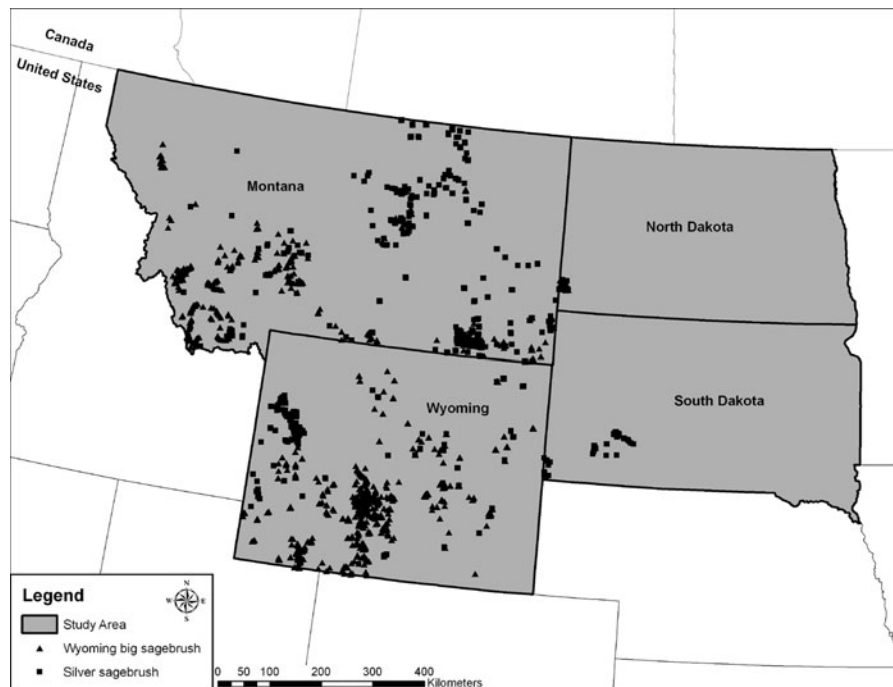
Fig. 1 Locations of sagebrush samples derived from the LANDFIRE dataset within the study area. *Circles* represent locations of Wyoming big sagebrush, and *squares* represent locations of silver sagebrush

Sagebrush distribution modeling: current climate data

Current climate variables were derived from the PRISM dataset (Daly et al. 1997). These data are available in a grid format and represent weather station data from remote locations that have been spatially interpolated across the landscape using techniques that incorporate elevational lapse rates (Daly et al. 1997). We used normals (i.e., the arithmetic mean of the variables over the three decades) for the time period from 1971 to 2000 for temperature and precipitation, which are available at 800-m resolution, to represent current conditions. We derived variables for seasonal average temperature and total precipitation, as well as average annual temperature and total precipitation, by combining monthly data to create seasonal and annual variables (Tables 1, 2).

Sagebrush distribution modeling: future climate scenarios

We obtained future climate data from the World Climate Research Programme (WCRP) Coupled Model Intercomparison Project (CMIP3). Data are available from the Intergovernmental Panel on Climate Change AR4 Report data archive. The data are

Table 1 List of climatic predictor variables and their relative contribution to the silver sagebrush distribution model

Climate variables	% Contribution
July precipitation	30.9
Summer (JJA) precipitation	23.8
January average temperature	7.9
July average temperature	6.7
Spring (MAM) precipitation	5.8
Fall (SON) average temperature	5.7
Fall precipitation	5.7
Winter (DJF) average temperature	4.5
Spring (MAM) average temperature	3.3
Annual average temperature	1.9
Annual precipitation	1.7
Summer (JJA) average temperature	1.4
January precipitation	0.4
Winter (DJF) precipitation	0.4

Variables represent the 1971–2000 normal for current climate and 2030 for future climate. Data are from Daly et al. (1997) and WCRP CMIP3 (Santa Clara University 2008)

Table 2 List of climatic predictor variables and their relative contribution to the Wyoming big sagebrush distribution model

Climate variables	% Contribution
July precipitation	44.5
Summer (JJA) precipitation	23.7
Spring (MAM) average temperature	7.2
January precipitation	4.9
Annual average temperature	3.6
Winter (DJF) precipitation	3.5
January average temperature	3.3
Fall (SON) average temperature	2.4
July average temperature	1.9
Winter (DJF) average temperature	1.7
Fall (SON) precipitation	1.2
Summer (JJA) average temperature	1.1
Spring (MAM) precipitation	0.7
Annual precipitation	0.3

Variables represent the 1971–2000 normal for current climate and 2030 for future climate. Data are from Daly et al. (1997) and WCRP CMIP3 (Santa Clara University 2008)

Table 3 GCMs included in this analysis

Model ID	Modeling group and country
CCC	Canadian Centre for Climate Modelling and Analysis, Climate Research Branch, Environment Canada
CSIRO	CSIRO Atmospheric Research, Australia
GFDL	US Department of Commerce, NOAA, Geophysical Fluid Dynamics Laboratory, USA
GISS	NASA, Goddard Institute for Space Studies, USA
NCAR	NSF National Center for Atmospheric Research, USA
UKMO	Hadley Center for Climate Prediction and Research, Met Office, UK

available on a monthly basis through the year 2099 from an original resolution of approximately 222 km^2 (2°) grid cells. Statistical downscaling was used to develop data sets at 12 km resolution (Maurer 2007).

We used six GCMs (listed in Table 3) to represent a suite of possible climate futures (Santa Clara University 2008). We selected GCMs based on the degree to which they successfully approximated past climatic conditions in the Pacific Northwest, northern Rockies and northern Great Plains (J. Escheid, personal communication). We assumed that the

ability of the model to accurately predict past conditions was the most reliable indicator of its ability to predict future climate conditions.

We modeled one future emissions scenario. We selected the SRES A1B scenario, which represents a "business as usual" future (Intergovernmental Panel on Climate Change 2007) and is commonly used in predictive distribution modeling studies. We chose one future time step—the year 2030—that represents a time both far enough in the future to allow for management action and close enough to the current year to be meaningful for managers. We obtained monthly average temperature and daily total precipitation grids for six GCMs and clipped grids to the study area. We converted daily precipitation into monthly precipitation by multiplying daily totals by the number of days in each month. We then derived seasonal and annual variables from monthly variables.

Sagebrush distribution modeling: data analysis

We used the Maxent method for modeling sagebrush bioclimatic envelopes under future climate scenarios. Maxent has recently been applied to bioclimatic envelope modeling and is particularly useful in situations where only presence data are available (Pearson et al. 2007; Raes and ter Steege 2007). Mathematical explanations for the method by which Maxent produces species distribution models, along with testing and validation of the approach, are found in Phillips et al. (2006). We chose Maxent as the analysis method because it is robust even with the inclusion of variables that are collinear (Evangelista et al. 2009).

We developed a layer of 10,000 background points to describe the suite of possible combinations of environmental variables within the study area (following Phillips et al. 2006). These background points aided model building by providing a backdrop against which the environmental conditions associated with presence point locations were evaluated. To test the ability of the model to predict an independent data set, we split the data set into two parts. We used 75% of the data to train the model and 25% of the data to test the model. We then used the value for the area under the receiver operating curve (AUC) for the test data set to determine how well the model would predict species distributions by comparing the model AUC value for the test data to the AUC value for a set of null models (methods described below).

Maxent allows the user to define the method by which the program fits the environmental layers (e.g., the climate layers described above) to constrain the probability distribution. The program has an "auto-features" option, whereby the user does not limit the fitting of the variables to one particular type of feature (e.g., linear, quadratic, hinge, threshold, product), but instead allows all types of features to be used. Previous studies suggest that overfitting can be a problem with large sample sizes ($n > 79$) using presence-only data and the auto-features option in Maxent (Raes and ter Steege 2007). Therefore, we ran the model using the following methods: (1) the auto-features option; and (2) using only linear, quadratic and hinge features. When using the auto-features option, the AUC for the model was inflated as compared with results when not using the auto-features option, suggesting overfitting of the model (Raes and ter Steege 2007). Therefore, we reported the results of the model using only linear, quadratic and hinge features, which serves as a more conservative estimate of the distribution of sagebrush habitat under current and future climate conditions.

We evaluated the model by comparing our results against a null model. Because we used only presence data to build the model, AUC values alone are not a suitable method for validating the accuracy of the model in differentiating between presences and absences (Pearson et al. 2007; Raes and ter Steege 2007). Our first step was to test for an environmental bias in our sampling locations, which we did by building 100 distribution models of 973 and 1,160 random points within the study area (15,500 total 12 km^2 cells). We then built another 100 distribution models with 973 and 1,160 points (to match the sample sizes for each species) within only the cells that originally had sagebrush presences recorded. We then compared the AUC values for the distribution model built on the random points to the distribution model based on the sample points drawn from our sample cell locations, and the values were significantly different ($p < 0.01$). This result indicated that we had an environmentally biased sample.

To ensure that we were comparing our environmentally biased model to a null model that took into account these environmental limitations, we created a bias-corrected null model against which to test our distribution model. We drew a random sample of points from the distribution of our original sagebrush

sample and repeated 100 times. This model is the bias-corrected null model. We then compared species distribution model AUC values to those AUC values from the bias-corrected null model for each species. We compared the AUC value from our model to the frequency histogram for the bias-corrected null model to determine if the distribution model AUC value fell outside the 95% confidence interval for the random model (Raes and ter Steege 2007).

West Nile virus spatial risk model

We developed West Nile virus transmission risk models by combining information on temperature thresholds for WNv transmission with predicted future temperature data from GCMs (as described above). We began by generating points in a regular array every 0.125 degrees across the study area to match the resolution of the GCM data, resulting in 4,690 data points. We used HydroGET, a web service client for ArcGIS, to download daily temperature minima and maxima at each point from the DAY-MET spatially interpolated climate dataset (Thornton et al. 1997) for the period January 1, 1980 through December 31, 2003. These dates represent the full extent of the DAYMET database.

Because the GCMs only provide average monthly temperatures rather than the daily temperature maxima and minima needed for the degree-day analysis of WNv transmission, we derived the future maximum and minimum temperatures as follows. First, we reduced the historical temperature data to 24-year mean maxima and minima for each month. We then used these values to calculate median monthly temperatures, which were compared to average monthly temperatures predicted by the GCMs. We calculated monthly maxima and minima for the GCM data by applying the difference between the extreme temperatures and the median temperatures of the historical data to the GCM data. For example, if historical July maximum and minimum temperatures were 30 and 16°C, respectively, with a median temperature of 23°C, the corresponding maximum and minimum temperatures for the same point in the GCM was found by adding and subtracting 7°C to the GCM average temperature.

We assessed the risk of WNv transmission using a degree-day model that uses historical and future daily maximum and minimum temperature (Zou et al. 2007). Due to data restrictions from the GCMs, every day of the month was assigned the same maximum and minimum temperatures. The model parameters most appropriate for the study area were calculated following Konrad et al. (2009) by spatially and temporally comparing sage-grouse deaths from WNv in northeastern Wyoming and south-central Montana with local temperatures during the days preceding the birds' deaths. We assumed a 12-day vector feeding period that equates to the sum of three four-day gonotrophic cycles (Reisen et al. 1993) and a minimum amplification threshold temperature of 14.3°C (Reisen et al. 2006; Zou et al. 2007). These values are appropriate for the mosquito *Culex tarsalis*, the primary arthropod vector of WNv in western sagebrush habitats (Turell et al. 2005). The sage-grouse data resulted in an estimate of 82 degree-days (DD) to complete the mosquito's extrinsic incubation period (EIP). This estimate is similar to the 76 DD calculated by comparison of WNv-killed crows and degree-day temperature in California (Konrad et al. 2009). The estimate of 82 DD fits the local WNv genotype and mosquito population as of 2006, but it should be noted that the WNv genotype has already changed since its introduction to the continental US in 1999 (Davis et al. 2005), and there is a possibility that future changes in the virus genotype or in the local mosquito species will have an unpredictable effect on virus transmission risk.

If the temperature over the course of the 12-day vector feeding period exceeds 82 DD, then WNv transmission is considered possible. Each grid cell was evaluated for each day of the year for both the historical and future temperatures. Data from the summer months (when both mosquitoes are active and warmer temperatures allow WNv transmission) are presented in this study.

Regional assessment model

To develop the regional assessment model, we reclassified cells into seven categories based on predicted future sagebrush distribution. We aggregated the distribution of the two species (from the maps in Fig. 2) by using the least presence threshold (Pearson et al. 2007) to distinguish between presence and absence. The least presence threshold requires calculation of the lowest predicted value associated with any presence point on the map; all values above

Fig. 2 a Models of current and future predicted climatically suitable conditions for silver sagebrush in 2030 using the Maxent modeling method, where *black* represents a probability of occurrence of 1.0 and *white* represents a probability of occurrence of 0.0, on a continuous scale of 0.0–1.0. Spatial resolution is 12 km. Model order is as follows: *a* current; *b* CCC model; *c* CSIRO model; *d* GFDL model; *e* GISS model; *f* NCAR model; *g* UKMO model. **b** Models of current and future predicted climatically suitable conditions for Wyoming big sagebrush in 2030 using the Maxent modeling method, where *black* represents a probability of occurrence of 1.0 and *white* represents a probability of occurrence of 0.0, on a continuous scale of 0.0–1.0. Spatial resolution is 12 km. Model order is as follows: *a* current; *b* CCC model; *c* CSIRO model; *d* GFDL model; *e* GISS model; *f* NCAR model; *g* UKMO model
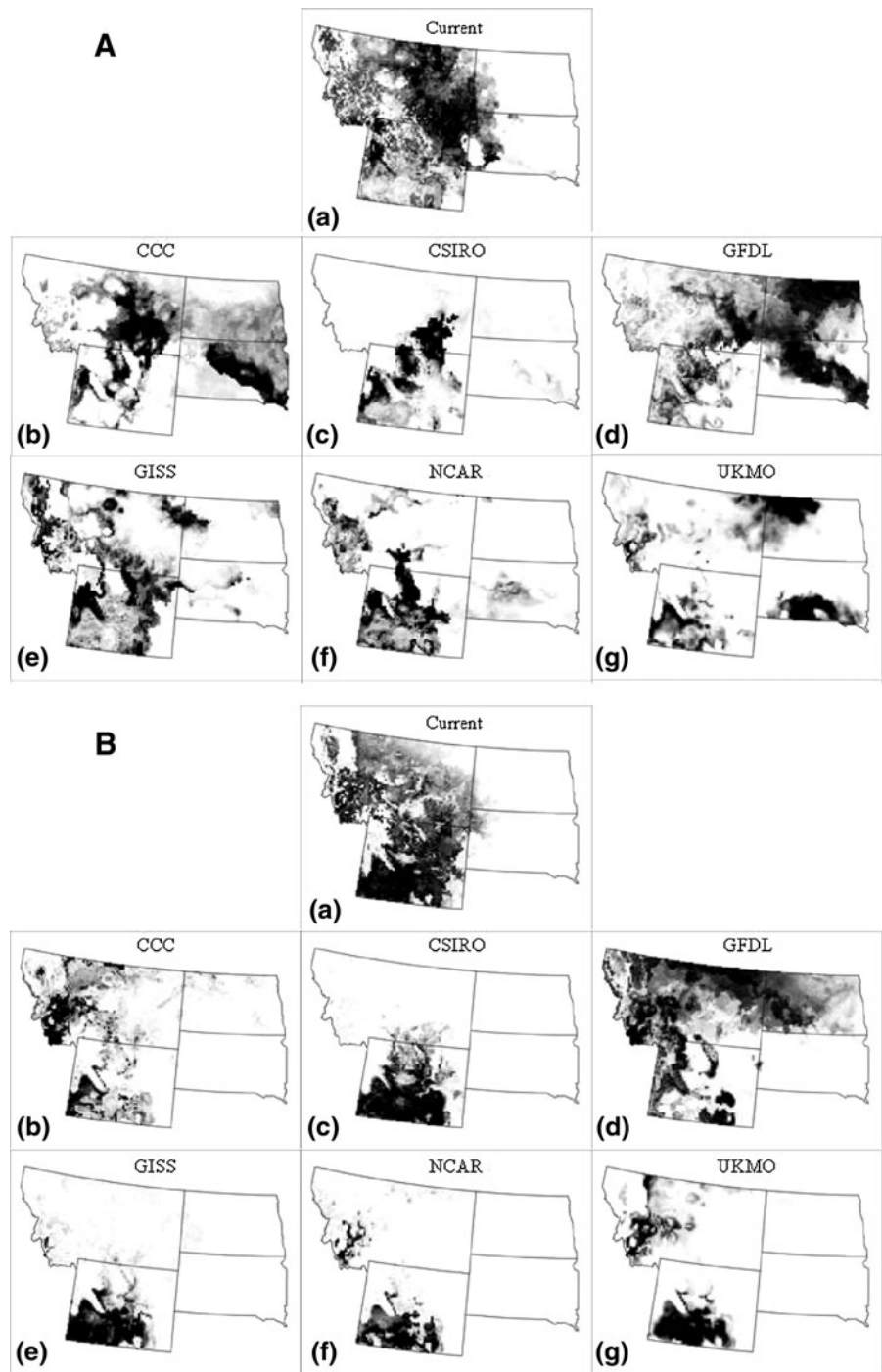
this threshold are classified as presences and values below this threshold are classified as absences. We then aggregated the results for each species, such that presence of either species resulted in presence of sagebrush for the entire cell. For WNv risk, we used a composite of risk across all three summer months and again reclassified cells as either at risk or not at risk over the three-month period. We created management

recommendations for each cell based on predicted future impacts of climate change on sagebrush and West Nile virus transmission risk. We developed this assessment only for Montana and Wyoming because we did not have WNv risk data for North and South Dakota.

Results

Sagebrush distribution modeling: trends and mapping

The species distribution models show a shift in the location of optimal bioclimatic conditions for sagebrush across the study area under the various future climate scenarios (Fig. 2). Summer (June–August) precipitation, and July precipitation in particular, was the variable most likely to influence the bioclimatic envelope for both species of sagebrush (Tables 1, 2). Silver sagebrush had the highest probability of occurrence in areas that receive between 100–150 mm of summer precipitation and between 35–50 mm in July, while Wyoming big sagebrush had the highest probability of occurrence in areas that receive <100 mm of precipitation in the summer and 15–40 mm in July. Models that predicted increases in precipitation, especially during the summer (e.g., CSIRO, NCAR), showed decreases in sagebrush by approximately 6%. The remaining models, which showed decreases in precipitation, showed overall stable to slight increases in sagebrush habitat (approximately 3–5%, except for CSIRO, which was an outlier at 21%).

All six models for silver sagebrush (Fig. 2a) showed a high probability of suitable bioclimatic conditions for sagebrush in some portion of the southwestern corner of Wyoming, and three of the models showed a high probability of suitable conditions in north-central Montana. For Wyoming big sagebrush (Fig. 2b), results were similar, but more dramatic. All six models showed suitable conditions in southwestern Wyoming, with three of the six models showing almost no suitable conditions outside of Wyoming. The remaining three models—CCC, GFDL and UKMO—showed suitable conditions in some areas of north-central Montana. Changes in the eastern part of the study area varied among models and were present in only one model (GFDL) for Wyoming big sagebrush (Fig. 2b). Three models—

CCC, GFDL and UKMO—showed climatic conditions suitable for silver sagebrush in eastern South Dakota (Fig. 2a).

Species distribution modeling: model evaluation

We evaluated the ability of the model to differentiate between presences and pseudo-absences by comparing the model AUC results to the bias-corrected null model AUC results. The silver sagebrush model had a training AUC of 0.942 and a testing AUC of 0.930, and the Wyoming big sagebrush model had a training AUC of 0.943 and a testing AUC of 0.935, both of which exceeded the 95% confidence interval cutoff for the bias-corrected null model. These results indicate that the sagebrush distribution models were significantly different from random and were able to discriminate between true presences and absences of sagebrush under current climatic conditions. We assume that this discriminatory ability holds for future climate scenarios.

West Nile virus spatial risk model

The results of the WNv transmission risk model showed an overall trend toward increasing transmission risk throughout the study area during peak transmission season (June–August). Five of the six models (all except CSIRO) showed increases in transmission risk in July, and four of the six models showed increased transmission risk in August (all except CSIRO and NCAR) (Table 4, Fig. 3).

Table 4 Percent change in area of transmission risk for West Nile virus in 2030 by GCM and month, compared to 1980–2003 average

Model	June	July	August
CCC	0.14	23.5	2.86
CSIRO	0	−30.19	−24.84
GFDL	56.1	57.87	51.79
GISS	0.02	16.83	22.43
NCAR	13.5	23.86	−4.99
UKMO	0.17	32.43	36.1

This model is based on data that suggest transmission after 82 degree days (Konrad et al. 2009) and was calculated using change in number of 12-km pixels between the two time frames
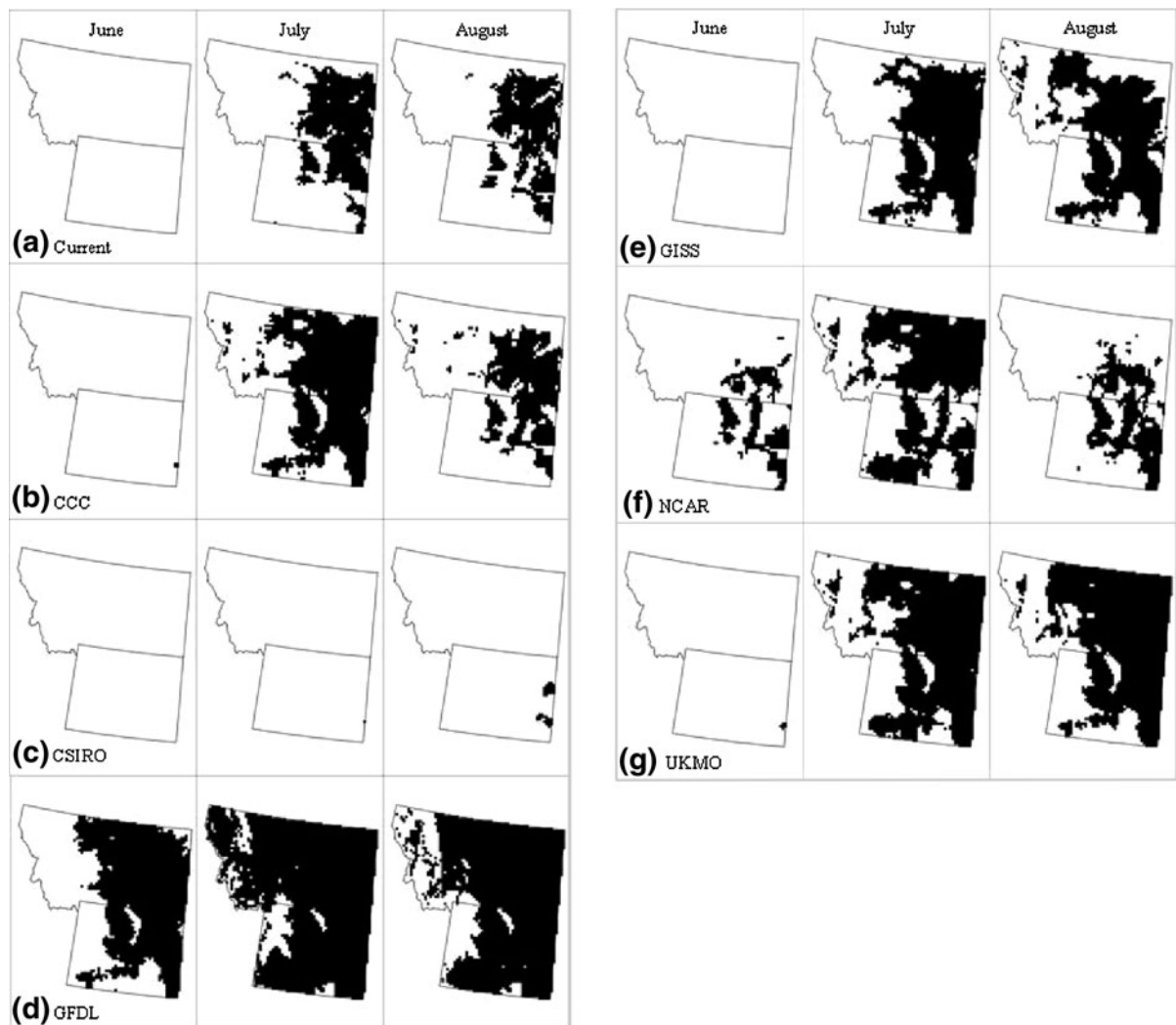
Fig. 3 Models of current and future predicted risk of WNv transmission in Montana and Wyoming using the degree-day model, where *black* represents probable transmission risk and *white* represents no transmission risk, on a binary scale of 1 and 0. Spatial resolution is 12 km. Model order is as follows:

a current June, July, August; *b* CCC model June, July, August; *c* CSIRO model June, July, August; *d* GFDL model June, July, August; *e* GISS model June, July, August; *f* NCAR model June, July, August; *g* UKMO model June, July, August

Changes in areal extent of transmission risk ranged from −30 to 58% depending on the model and month. Overall trends among the models (not including CSIRO) indicate possible increased risk in June, substantial increased risk in July and moderate to substantial increased risk in August. Spatial examination of the risk surface revealed increased transmission risk further west and at higher elevations, including portions of the northern Rockies not currently believed to be substantially affected by the virus (Naugle et al. 2005; Walker and Naugle

2010). Under all models except CSIRO, transmission risk increased in southwestern Wyoming in locations identified as climatically suitable core habitat for sagebrush (Fig. 3).

Regional assessment model

We present a composite assessment of future climate impacts on sagebrush distribution and WNv risk (Fig. 4) and provide management recommendations based on predicted future changes in habitat and
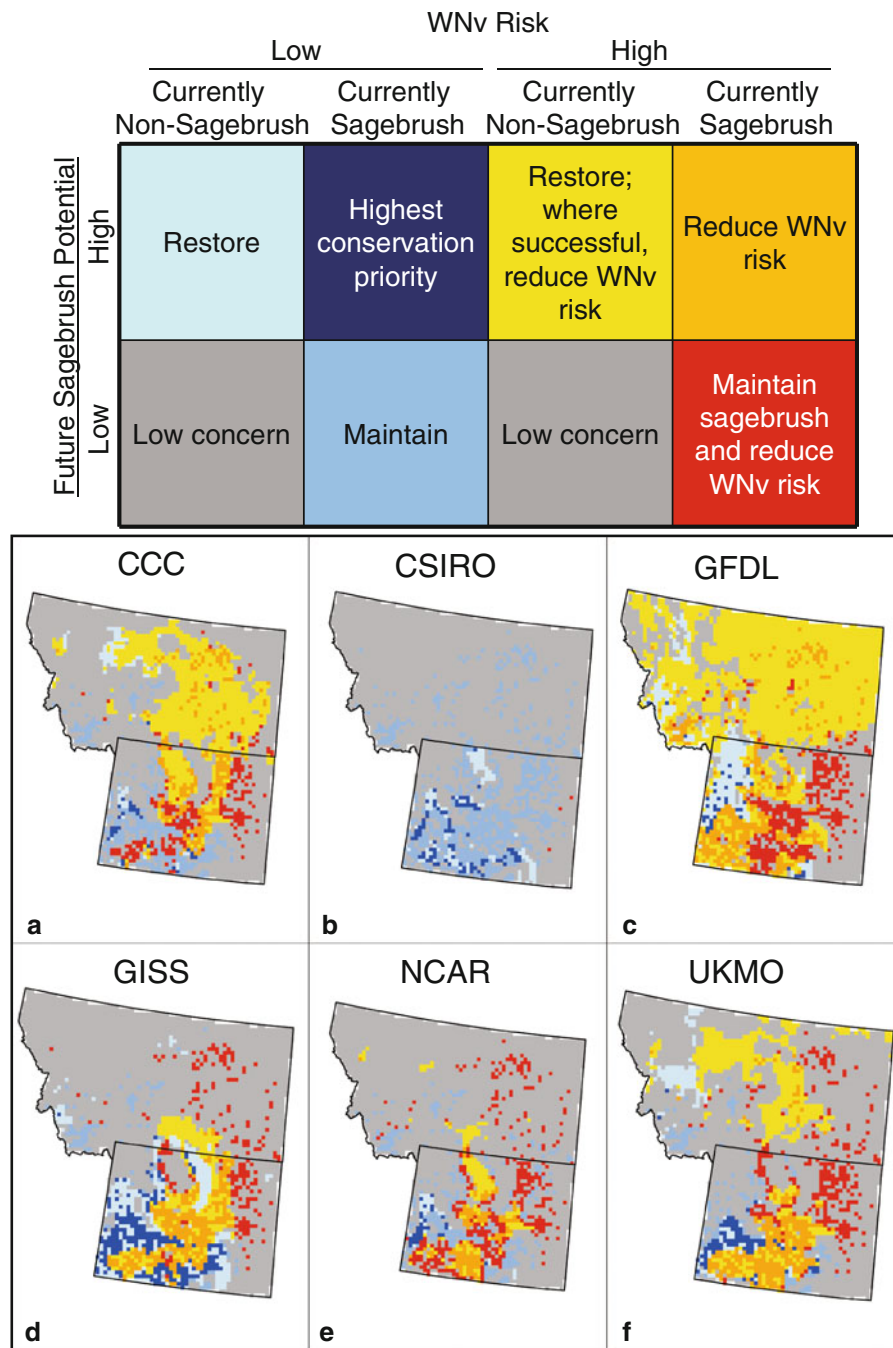
Fig. 4 A regional composite assessment of future habitat and disease risk across the study area. *Colors* represent different combinations of current habitat availability, predicted future climatic conditions for sagebrush, and predicted future WNv risk, along with management recommendations for each scenario, which are outlined in the "Discussion"

disease risk for greater sage-grouse. This assessment suggests that high-elevation sagebrush habitat in southwestern Wyoming (dark blue areas; Fig. 4) is of the highest conservation concern and should be the

primary focus of resources for protecting current sagebrush habitat. These areas currently have sagebrush and are likely to be highly suitable for sagebrush and have a low risk of WNv transmission

in the future. Neighboring areas of southwestern Wyoming and Montana are good candidates for maintaining current sagebrush populations and limiting competing threats (e.g., energy development) into the future (medium blue areas; Fig. 4). Restoration projects have the highest potential for success in western Wyoming in most models and in north-central and northwestern Montana in some models. Some portions of these areas do not currently have robust sagebrush habitat but likely will have climatic conditions necessary for sagebrush establishment in the future (light blue areas; Fig. 4). Management practices that reduce transmission of West Nile virus will become increasingly important throughout most of Wyoming and eastern Montana. These areas have and will continue to have suitable conditions for sagebrush, but also have a high risk of WNv transmission (orange areas, Fig. 4). Restoration projects could be beneficial in the Bighorn area on the Montana-Wyoming border and in much of eastern Montana that currently lacks sagebrush. Areas where restoration is successful should be managed to reduce WNv transmission (yellow areas; Fig. 4). In eastern Wyoming and portions of southwestern Wyoming, decreasing WNv transmission should be a priority, with restoration of degraded habitat occurring where possible (red areas; Fig. 4).

Discussion

Predictive models of climatically suitable habitat for sagebrush and high-risk areas for WNv transmission in the face of predicted future climate change provide important information to aid in the conservation of imperiled, sagebrush-dependent species, such as greater sage-grouse. Our results suggest there will be changes in the location of climatically suitable conditions for sagebrush by 2030, with key areas located in southwestern Wyoming, north-central Montana and possibly northeastern Wyoming.

One method for qualitatively evaluating the results of species distribution models is to examine if the important predictor variables coincide with known drivers of current and historic distributions of the species. The results of this study support known historic distributions of sagebrush in relation to climate, and paleoecological data document the occurrence of sagebrush in cold, dry regions. The presence of sagebrush pollen is characteristic of arid landscapes that are climatically dominated by low precipitation and low winter temperatures and is representative of an arid, "winter-cold desert" landscape (Wells 1970). Sagebrush pollen was shown to increase during times of "maximum aridity", which occurred from 8,000 to 4,000 years BP in the prairie regions of the northern plains of the US (Clark et al. 2001). Recent studies on the relationship between semi-arid shrubs and precipitation show that summer drought favors deep-rooted shrubs over more shallow-rooted grasses and forbs (Schwinning et al. 2005). It should be noted that species distribution models for cheatgrass have suggested that decreasing summer precipitation may lead to increased suitable climatic habitat for cheatgrass by creating a competitive advantage over native shrubs and grasses whose growth rates are tied to summer moisture availability (Bradley 2009). However, our study suggests that, within certain summer precipitation ranges, suitable climatic habitat for sagebrush may increase.

The results of our WNv transmission risk model suggest that the virus may spread to previously uninfected areas at high elevations in the western portion of our study area. The westward spread of WNv may also be facilitated by coalbed methane development and the associated standing water that provides habitat for mosquitoes (Doherty 2007; Zou et al. 2007). This threat may increase in the future because coalbed methane drilling locations are found at higher elevations in southwestern Wyoming. The majority of the models showed slight to substantial increases in transmission risk early in the transmission season (June and July), suggesting that earlier infections and deaths due to WNv in greater sage-grouse are likely.

Although we used statistically downscaled climate models to develop these species distribution models, the feasibility of making management decisions on the ground using 12 km resolution data should be acknowledged. For instance, while the results of our sagebrush models agree with both historic and current distribution data, models based on precipitation must be interpreted with caution. Future predicted values of precipitation, which drive the sagebrush bioclimatic envelope model, are generally considered less accurate than future predicted temperature values (Canadian Institute for Climate Studies 2010). Scientific consensus abounds on predicted increases in

future temperature and, therefore, the results of our temperature-driven WNv model may be interpreted with more certainty. There are several factors that contribute to virus transmission, including mosquito abundance, virus reservoirs, amplifying hosts and larval habitat; however, we use temperature as a critical and limiting factor as a proxy for virus transmission risk. One of the six future climate scenarios (CSIRO) showed decreases in transmission risk because average summer monthly temperatures were predicted to decrease. This result is somewhat counterintuitive, and may be due to either error in the predictive capability of the original GCM or error associated with downscaling the GCM results to 12 km resolution (Maurer 2007). In addition, making decisions on a local scale using 12 km resolution data can be challenging, as predictions in one particular cell of the model may not translate to what is occurring on the ground. We acknowledge these limitations and suggest that the results be applied in a predictive, regional context and that monitoring trends in both species distributions and West Nile virus occurrence across the landscape will help to inform on-the-ground decision making on shorter time scales and smaller spatial scales.

Sagebrush is a long-lived plant that may persist on the landscape for up to a century following the onset of unsuitable climatic conditions (Howard 1999). Thus, decreases in suitable climatic habitat, as shown in this study, do not necessarily indicate the elimination of individuals from the landscape, but rather climatic conditions that are less conducive to the long-term survival and reproduction of the species. Alternatively, predicted species occurrence does not necessarily equate to species persistence on the landscape. The sagebrush community may have been increasing or decreasing during the initial collection of location data, which could lead to false negative or false positive predictions, respectively (Wilson et al. 2005). Moreover, in the face of increasingly unsuitable climatic conditions, disturbance, such as fire or mechanical destruction of sagebrush, could lead to a situation where sagebrush recovery is highly unlikely following the disturbance event. In addition, bioclimatic envelope models ideally are built using the entire distribution of the species; however, in this case, we were particularly interested in understanding impacts in a specific area of the distribution and, thus, focused our efforts there. We acknowledge that this

decision limits our ability to draw inference outside of our study area, as not all of the climatic conditions under which sagebrush has established are represented in our sample.

Cumulative impacts of predicted climate change on sagebrush habitat and West Nile virus transmission are likely to reduce suitable sage-grouse habitat in the northern Great Plains and northern Rockies. However, we can identify two conservation priorities for greater sage-grouse. The spatial representations of the "best available" habitat for the sage-grouse, both currently and twenty years in the future, indicate that areas in southwestern Wyoming will serve as important core refugia for sage-grouse populations, due to persistent sagebrush habitat, but will also experience elevated risk for West Nile virus transmission. Areas in north-central Montana are considered important fringe populations because they are located near the northern extent of the bird's range and currently contain intact sagebrush habitat. Dispersal pathways (e.g., intact sagebrush habitat) that connect these populations and the core population in southwestern Wyoming should be protected. Peripheral sage-grouse populations are more likely to be extirpated than populations that inhabit core areas, and these populations may contain location-specific adaptive capacity that could contribute genetic diversity to the species as a whole (Fig. 4; Lesica and Allendorf 1995; Channell and Lomolino 2000; Guo et al. 2005; Aldridge et al. 2008).

Our results support a regional-scale approach to conserving greater sage-grouse in the face of numerous threats to their long-term viability. Implementing measures to secure sage-grouse habitat in those areas where our models predict the highest probability of persistence will allow for the most efficient and effective use of limited conservation resources (Pressey et al. 2007). Greater sage-grouse in some parts of our study area migrate long distances (>60 km) between seasonal habitats (Connelly et al. 2004; Tack 2006). Thus, protecting not only those core areas with the highest probability of persistence, but also those areas that will maintain connectivity between core areas will be an important management strategy for this species (Tack 2006).

Allowing wildlife to adapt to climate change is often spoken of in terms of resilience (Millar et al. 2007). Successful conservation in the face of climate change, which could exacerbate habitat loss and

increase disease risk, will require reducing other stressors on the population. We recommend increased emphasis on conservation and protection of areas with a high probability of suitable sagebrush habitat in the future, including both core and peripheral areas. Within those areas, proactive management of anthropogenic water sources will be required to reduce the spread of mosquitos that transmit West Nile virus. In addition, restoring converted areas back to native sagebrush-steppe and preventing widespread loss of sagebrush habitat to new development (energy, urban, residential, agricultural, etc.), particularly along the range periphery (Aldridge et al. 2008), will be important. We may also promote long-term resilience to change by maintaining habitat within dispersal corridors between fringe and core populations. Finally, to determine the effectiveness of these measures, regional monitoring programs should be implemented that can identify when thresholds are about to or already have been surpassed in order to prompt appropriate conservation or regulatory action.

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