FINAL REPORT: KEYSTONE SPECIES HABITAT SUITABILITY MODEL (PART 1)

STATE: Kansas
GRANT NUMBER: W-108-R-1
GRANT TITLE: HOMES ON THE RANGE: Identifying potential landscapes for conservation across the grasslands of North America: Integrating keystone species, land use patterns, and climate change to enhance current and future grassland restoration efforts

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INTRODUCTION

Because prairie dogs function as ecosystem engineers and keystone species in North America's grasslands (Fig. 1), their conservation and management lies at the core of many conservation efforts. However, prairie dog management is challenging because they are severely affected by epizootic plague outbreaks caused by the introduced bacterium *Yersinia pestis*[1], and highly threatened by drought and climate change in the southern portion of their range[2–4]. In fact, the formerly-largest remaining colonies (in Janos, Chihuahua, Mexico and Conata Basin of South Dakota, USA) have collapsed by 50-90%, in just over the last 10 years, largely due to plague, drought, and land use impacts. This underscores the urgency for conserving prairie dog colonies, associated species, and mitigating plague and impacts from climate and land use change by identifying potential landscapes for conservation action, both now and into the future. And,–critically–such areas need to be considered within the context of rangelands that

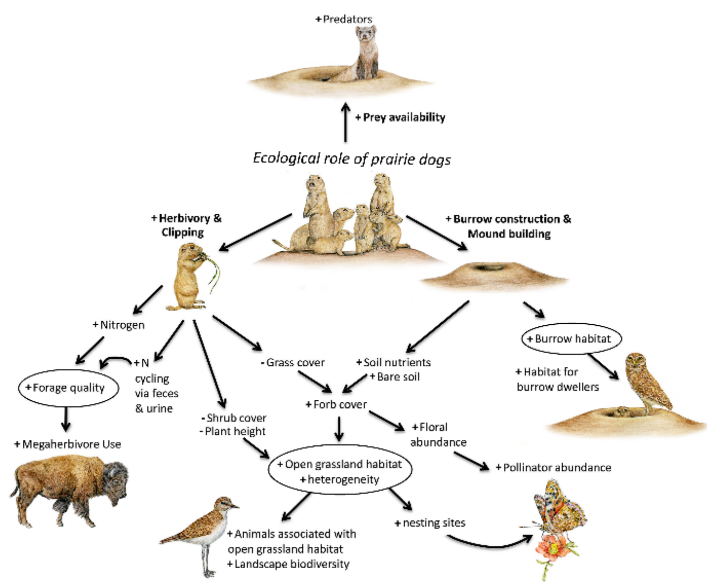

Fig. 1. *Conceptual diagram illustrating how the ecological role of prairie dogs cascades throughout the prairie dog ecosystem. Plus signs indicate an increase in an ecosystem property as a result prairie dogs; minus signs indicate a decrease. (Modified version from Davidson et al. 2012* [2]*)*

are relied on for cattle production and have traditionally harbored complex social cultures resistant to prairie dog conservation.

The capacity for a landscape to support spatially extensive grassland conservation efforts depends on a complex suite of abiotic, ecological, social, and economic factors. Mapping of landscape capacity to support such conservation efforts in the central Great Plains can provide a much-needed tool for optimizing use of scarce funds for grassland conservation and restoration efforts. This is especially valuable for contemporary management because of the social, environmental, and economic factors that influence where prairie dog complexes can be conserved and expanded across large blocks of continuous habitat – to support numerous grassland species.

To address this need, we are working to identify potential landscapes for conservation, through spatial modeling. Our work is examining ecological, political, and social factors, along with changing climate and land use to maximize long-term conservation potential and co-existence with human activities. Our project involves two major components: Part I, developing a black-tailed prairie dog habitat suitability model (HSM) under both current climate and projected future climate scenarios (Fig. 2) and Part II, identifying suitable landscapes for black-tailed prairie dog (BTPD) ecosystem conservation using the conservation planning tool, Zonation. Here we provide the Final Report for the BTPD HSM (Part I) (Fig. 2).

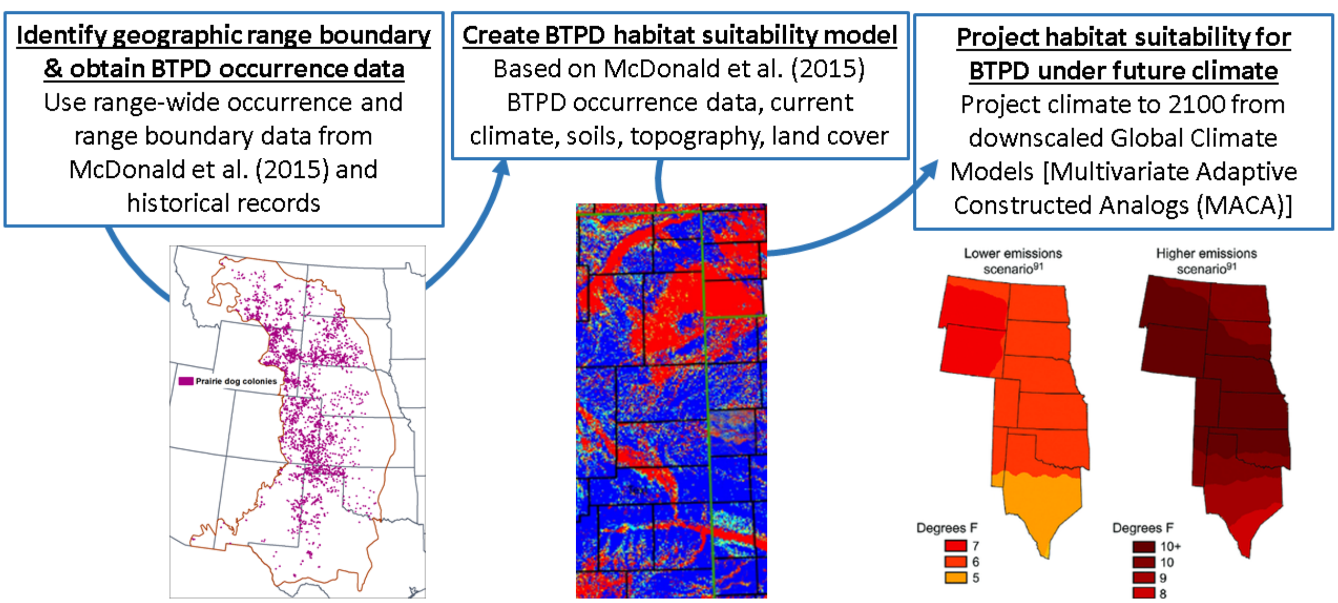

Fig. 2. *Methodological approach for developing the black-tailed prairie dog habitat suitability model (HSM).*

METHODS

To begin Part I of our analysis, we first obtained BTPD occurrence data and identified their geographic range boundary (Fig. 2). We obtained range-wide prairie dog occurrence data from Western EcoSystems Technology, Inc. (WEST, Inc.; Hereafter, "WEST data") to use for our primary HSM analysis because colony data was systematically collected across the BTPD range over the same time period[5]. The WEST data is based on prairie dog colonies identified using National Agriculture Imagery Program (NAIP) imagery from a stratified random sample of 2x2mile grid cells extending across the BTPD range within the United States. (Table 1.).

Table 1. Sample size of the WEST data[5]. The Table below is Table 1.1 from McDonald et al. (2015), showing total number of 2 mi by 2 mi grid cells in each state or overlapping BLM managed land, number of grid cells sampled (sample size) and date of National Agriculture Imagery Program (NAIP) imagery.

State	Sample size	Total number of cells	Date of NAIP Images
Arizona	477	2,361	2013
BLM	2,422	21,790	2012, 2013, 2014
Colorado	1,122	11,101	2013
Kansas	1,034	12,785	2014
Montana	1,318	16,302	2013
Nebraska	1,128	13,960	2014
New Mexico	1,362	16,852	2014
North Dakota	1,012	5,011	2014
Oklahoma	1,078	8,888	2013
South Dakota	1,230	12,165	2014
Texas	1,982	24,539	2014
Wyoming	1,722	8,790	2012

In order to transform the WEST data into a format suitable for data analyses, we generated presence and absence points for BTPD using the WEST data. For each colony polygon detected within a given grid cell, we assigned one presence point for each hectare within the colony and then randomly selected one absence point for every 15 ha within the remaining portion of the grid cell where no colonies were found. All points were at least 60 m (two 30 x 30 m raster cells) away from each other, and all absence points were at least 500 m from any presence point. This produced approximately 86,300 presence points and 315,000 absence points, from which we randomly selected the same number of absence points as presence points to use in our HSM analysis.

Our BTPD range boundary is based on current and historical distribution. To determine current range we largely followed the WEST[5] boundary and extended the range boundary where appropriate to reflect the historical range distribution based on museum specimens. Each states' Western Association of Fish and Wildlife Agencies (WAFWA) Prairie Dog Conservation Team (PDCT) member approved the Final BTPD boundary for their state, and GPS point locations for all museum specimens we used to create our boundary are stored in our project database along with detailed metadata for each.

The next step in our Part I modelling effort involved determining the best and most current spatial data layers available for soils, climate, topography, and land cover for the HSM (Tables 2 and 3 and Fig. 3). We downloaded and processed data for analyses (described below), and identified suitable land cover types and patch metrics. These efforts yielded a total of 25 environmental input datasets for the full study area, based on the data sources in Table 2 (see also Fig. 3).

Our research team identified and obtained several valuable databases representing major improvements in the resolution and accuracy of the input variables. First, we obtained the 2016 National Land Cover Database (NLCD), which was released by USGS in May of 2019. This 2016 database represents a major improvement from 2011 NLCD that was previously available, as it incorporates new data derived from the USDA's Cropland Data Layers for 2011 – 2016, and implemented new algorithms for identifying developed and paved surfaces. Second, rather than using the National Soil Survey's SSURGO database to map soil types across the BTPD range, we used a new digital soil map of the US (POLARIS [6,7]) that builds upon SSURRGO but includes improved interpolation of soil texture and other attributes down to a 30-m pixel resolution. One limitation is that this improved soils model did not include depth to bedrock, which is an important factor influencing BTPD burrowing. We attempted to use the latest SSURGO soils data[8] for the depth to bedrock metric, compiling depth to bedrock values from individual statewide datasets and averaged over map unit components. Many map units had no bedrock depth measure in SSURGO, so we estimated missing data using a component-weighted average of maximum horizon depth. Polaris soils data[7] are available as individual 1-degree tiles per metric per depth, so we downloaded, depth-weighted, and merged the Polaris data by soil metric over the study area. The most recent National Elevation Data (NED)[9] was likewise downloaded as individual 1-degree tiles and merged over the study area. We then corrected the NED by identifying and removing as many sink artifacts as possible, while preserving true sinks such as playas and perennial water bodies. Next, we used the software TauDEM[10] to calculate a Topographic Wetness Index as well as slope for the entire BTPD range. The NED was also used to create a Terrain Ruggedness Index as well as information on aspect as a function of 'northness' and 'eastness'. We used the 2016 NLCD[11] as the basis of several land cover type metrics including patch size, distance to patch edge, and nearest edge type. Finally, current climate data metrics were calculated from raw daily gridded meteorological data[12] averaged over 1994 - 2014. All continuous datasets were normalized to be between 0 and 1 (-1 to +1 in the case of the northness and eastness measures) so that inputs had equivalent scales. Categorical data (primarily land cover) were converted to one-hot 'dummy' variables for use in modeling algorithms that cannot accept categorical inputs. The Python and R scripting code written for many of the above calculations is available at https://github.com/mmfink/HOTR_Code. TauDEM, which is written in C++, is available at http://hydrology.usu.edu/taudem/taudem5/. The remaining data processing was done in ESRI ArcGIS. During iterative modeling, we narrowed down environmental inputs based on covariate correlation, proportion of deviance explained, and effect on model performance (Table 3). We were forced to drop the SSURGO-derived depth to bedrock input due to the large amount of data coded as zeroes (indicating no real depth data available), which was biasing model output.

Table 2. *Spatial data layers and their sources used in the black-tailed prairie dog (BTPD) habitat suitability model.*

Variable	**Spatial data layer for Habitat Suitability Model**
BTPD colony occurrences	Prairie dog occurrences from WEST survey[5]
Land Cover	USGS National Land Cover Database 2016[11]
Soils	POLARIS 30-m resolution database[7] Metrics: bulk density to 100cm, Sand to 100cm, %Clay to 100cm, % organic matter to 100cm, pH to 100cm
Slope & elevation	National Elevation Dataset[9] Metrics: Topographic Wetness Index, Topographic Ruggedness Index, slope, aspect
Climate – current	Current climate (1994-2014), using gridMet[12] Metrics: Mean annual precipitation (mm), winter + spring & summer + fall precipitation, max summer temperature, potential evapotranspiration, growing degree days
Climate – future (used only for HSMs projected into the future)	Future Climate (2100), using MACAv2_METDATA[13,14] Metrics: Mean annual precipitation (mm), winter + spring & summer + fall precipitation, max summer temperature, potential evapotranspiration, growing degree days

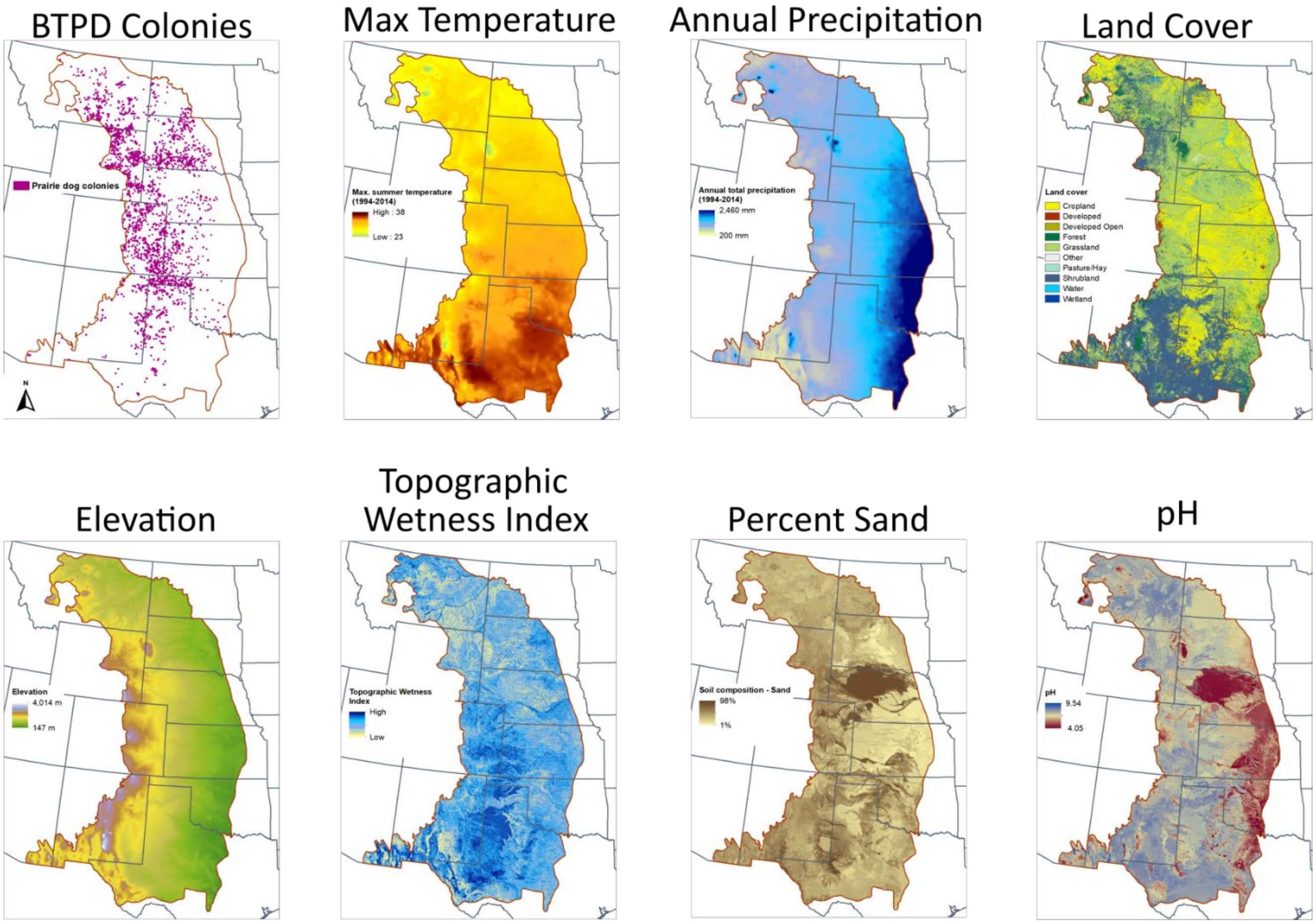

FIG. 3. *Some of the spatial layers created for the black-tailed prairie dog (BTPD) habitat suitability model, based on BTPD occurrence*[5]*, climate*[12]*, land cover*[15]*, topography*[9]*, and soils*[7]*.*

To determine the best-fit habitat suitability model for our data, we evaluated the performance of several different independent models and an ensemble model[16,17]. Specifically, we created BTPD habitat suitability models using a: 1) Generalized Linear Mixed-Model (GLMM), 2) Random Forest model (RF), 3) Boosted Regression Trees model (BRT, also known as Generalized Boosted Models or GBM), and 4) an ensemble model that combined the outputs of the GLM, BRT, and RF HSMs. Models were created using the R packages *lme4*[18], *randomForest*[19], and *dismo*[20]. The GLMM used the identity of the sampling grid cell that each presence or absence point fell within as a random factor. All R code used for modeling is available at the previously mentioned GitHub repository.

Table 3. *All environmental inputs considered, with the final used in bold (in "Label" column).*

Label	Description	Based On
bd	soil bulk density to 1 m (g/cm3)	POLARIS
clay	percent clay to 1 m	POLARIS
DEM	elevation (m)	USGS NED
depth	depth to bedrock (cm)	SSURGO
distToNon	distance (from each pixel) to the nearest non-habitat (m)	NLCD 2016
eastness	east-west aspect index	USGS NED
GDD5	annual growing degree-days, base 5, averaged over 1994-2014	gridMET
hab_non	binary designation of grass/shrub habitat (1) or other land cover type (0)	NLCD 2016
hab_nonpch	patch size of contiguous habitat or non-habitat (m2)	NLCD 2016
nearType	land cover type of the nearest non-habitat (categorical)*	NLCD 2016
nlcd	land cover (categorical)*	NLCD 2016
nlcd_patch	patch size of each land cover type (m2)	NLCD 2016
northness	north-south aspect index	USGS NED
om	percent organic matter to 1 m	POLARIS
PET	annual potential evapotranspiration, grass reference (mm), averaged over 1994-2014	gridMET
ph	soil pH to 1 m (soil:water method)	POLARIS
ppt_sf	summer – fall (June-November) total precipitation (mm), averaged over 1994-2014	gridMET
ppt_ws	winter – spring (December-May) total precipitation (mm), averaged over 1994-2014	gridMET
ppt_yrly	annual total precipitation (mm), averaged over 1994-2014	gridMET
sand	percent sand to 1 m	POLARIS
slope	degrees slope	USGS NED
tmax	maximum summer (June-August) air temperature, averaged over 1994-2014	gridMET
TRI	Terrain Ruggedness Index	USGS NED
TWI	Topographic Wetness Index	USGS NED

*Categorical variables were converted into one-hot dummy variables (e.g., nlcd.Grassland, nlcd.Cropland, etc.) for the GLMM model.

Models were trained on a random 70% subset of the full dataset, maintaining relatively equal numbers of presence and absence points (Fig. S1). Half of the remaining data (15%) were used to evaluate RF and BRT model performance during tuning of the calling parameters (such as number of trees). The final 15% of withheld data ("Testing dataset") were then used to evaluate all three final models (Table S1, Fig. S1). All sampling of presence/absence points was done at the level of the grid cell (i.e., the cells were randomly sampled, not the points within them). We selected 95% Sensitivity because our primary goal was to correctly identify prairie dog habitat.

The ensemble model was created as a weighted average of the final GLMM, RF, and BRT models. Using the *mean* of Sensitivity=0.95, weights used were calculated by averaging 6 performance metrics (AUC, TSS, PCC, Kappa, Sensitivity, and Specificity), which were themselves averaged over a 10-fold cross-validation of the models built on the Training dataset. This gives the higher performing models more influence over the ensemble. For the cross-fold validation, each fold randomly sampled 10% of the sampling grid cells in the Training dataset, so that if a sampling grid cell was selected, all presence and absence points within that cell were assigned to that fold. The ensemble was evaluated against the Testing dataset as well (Table S1).

BTPD Habitat Suitability Model under Future Climate

Next, we projected our BTPD HSM into the future (2100) under two different (representing "best" and "worst case") climate scenarios: 1) warm and wet (IPSL-CM5A-LR_r1i1p1_rcp45); and 2) hot and dry (MIROC5_r1i1p1_rcp85). These models best represented the two scenarios for our study region. The future climate model scenarios were obtained from MACA v2-METDATA, and were averaged over 2076-2099 (Table 2). All other model inputs remained the same. From the MACA website, "Climate forcings in the MACAv2-METDATA were drawn from a statistical downscaling of global climate model (GCM) data from the Coupled Model Intercomparison Project 5 (CMIP5, Taylor et al. 2010) utilizing the Multivariate Adaptive Constructed Analogs (MACA[13]) method with the METDATA[26] observational dataset as training data."

Ensemble Model Review

During summer 2020, our team met with biologists from each State individually and with other experts on the prairie dog ecosystem to provide detailed State-level review of the ensemble habitat suitability map. After extensive review, our team worked to address each of the comments we received. The biggest challenge our team faced was modelling the desert grasslands of the American Southwest (AZ, southern NM, southwestern TX), where prairie dogs occurred historically, and considerable grassland remains. But throughout this region, prairie dogs were extensively exterminated over the last century and their populations have not recovered as in other parts of their range, likely due to the increasingly arid climate and grassland desertification[21–24]. Nevertheless, extensive grassland remains in the region and colonies do exist, just not in high enough abundance to be well-sampled by the WEST et al. effort. To help address this, we obtained additional, recent data (within the last ca. 10 years) for AZ, NM, and TX from within the desert grassland ecoregion[25] to add to the occurrence locations identified in the WEST data. This allowed us to better model habitat conditions where BTPDs occur across the desert grassland ecoregion. We randomly selected the same number of grid cells in the WEST et al. data and traded them out with the new grid cells covering the additional occurrence data. This way we were able to retain the same number of grid samples per state. To account for the higher level of sampling effort in Wyoming and Colorado in the WEST[5] study, we randomly sampled an equal density of grid cells in each state across the BTPD geographic range. We also removed errors in occurrence data identified during the reviews by biologists in each State, as some of the occurrences were false positives. In a few instances along the western edge of the BTPD range in New Mexico, we removed mapped colonies that were likely to be Gunnison's prairie dogs rather than BTPD, based on consultation with the state wildlife agency.

RESULTS

Habitat Suitability Model

Among the three models used the build the ensemble SDM, GLMM performed most poorly and was more restrictive in identifying suitable prairie dog habitat than RF and BRT (Table S1; Fig. S1). Yet, GLMM performed better at modelling suitability relative to soils across the BTPD range compared to RF and BRT, while RF and BRT modelled suitability relative to climate better than GLMM. Climate variables were important predictors across all models, followed by topography and landcover; soils were generally less important (Fig. S2). The variables of greatest importance for the GLM were: topographic ruggedness, growing degree days, and soil organic matter; whereas variables of greatest importance for both the RF and BRT were: summer-fall precipitation, growing degree days, winter-spring precipitation, landcover, and topographic ruggedness (Fig. S2).

When we compared performance metrics of all four models (GLMM, RF, BRT, ensemble), the Random Forest model performed slightly better than the ensemble, followed by BRT and GLMM (Table S1; Fig. S1). However, we selected the ensemble model to build our SDM because not only did it perform similarly well to RF, but it also made ecologically most sense when we evaluated each of the models independently and the ensemble SDM appeared to reduce the impact of individual model biases. Indeed, ensemble SDMs often perform better than single SDMs because they can average out uncertainties and biases inherent in different model algorithms. Our final ensemble model exhibited high predictive accuracy, with an AUC of 0.96 and error rate of 13% at a Sensitivity (ability to correctly identify prairie dog habitat) of 95% (Figs. 4 and S3). We also evaluated the model when Sensitivity was equal to Specificity and when Specificity was 95% and found similar model performance (Table S3; Fig. S3).

The most suitable habitat for the BTPD ecosystem under the current climate extends largely from northern and eastern New Mexico and the panhandle of Texas and Oklahoma through eastern Colorado, eastern Wyoming, southern Montana, western south Dakota, and parts of western Kansas and Nebraska (Fig. 5, Table 4). Small patches of suitable habitat occur through the southwest in Arizona, southern New Mexico, and southwest Texas. The eastern part of the original prairie dog range is largely unsuitable due to the extensive conversion of grassland to cropland, and the southern portion of their geographic range is limited largely by climate suitability. Low suitability across most of Nebraska is due to excessively sandy soils.

Model	AUC	TSS	kappa	PCC	Sensitivity	Specificity	Error rate
Ensemble	0.96	0.75	0.75	0.87	0.95	0.80	0.13
		True Skill Statistic TSS = TPR + TNR − 1		Percent correctly classified	ability to correctly identify **prairie dog habitat** (true positive rate)	ability correctly identify **non-prairie dog habitat** (true negative rate)	

Fig. 4. *Performance metrics of the black-tailed prairie dog ensemble habitat suitability model. These performance metrics reflect when Sensitivity is set to 0.95.*

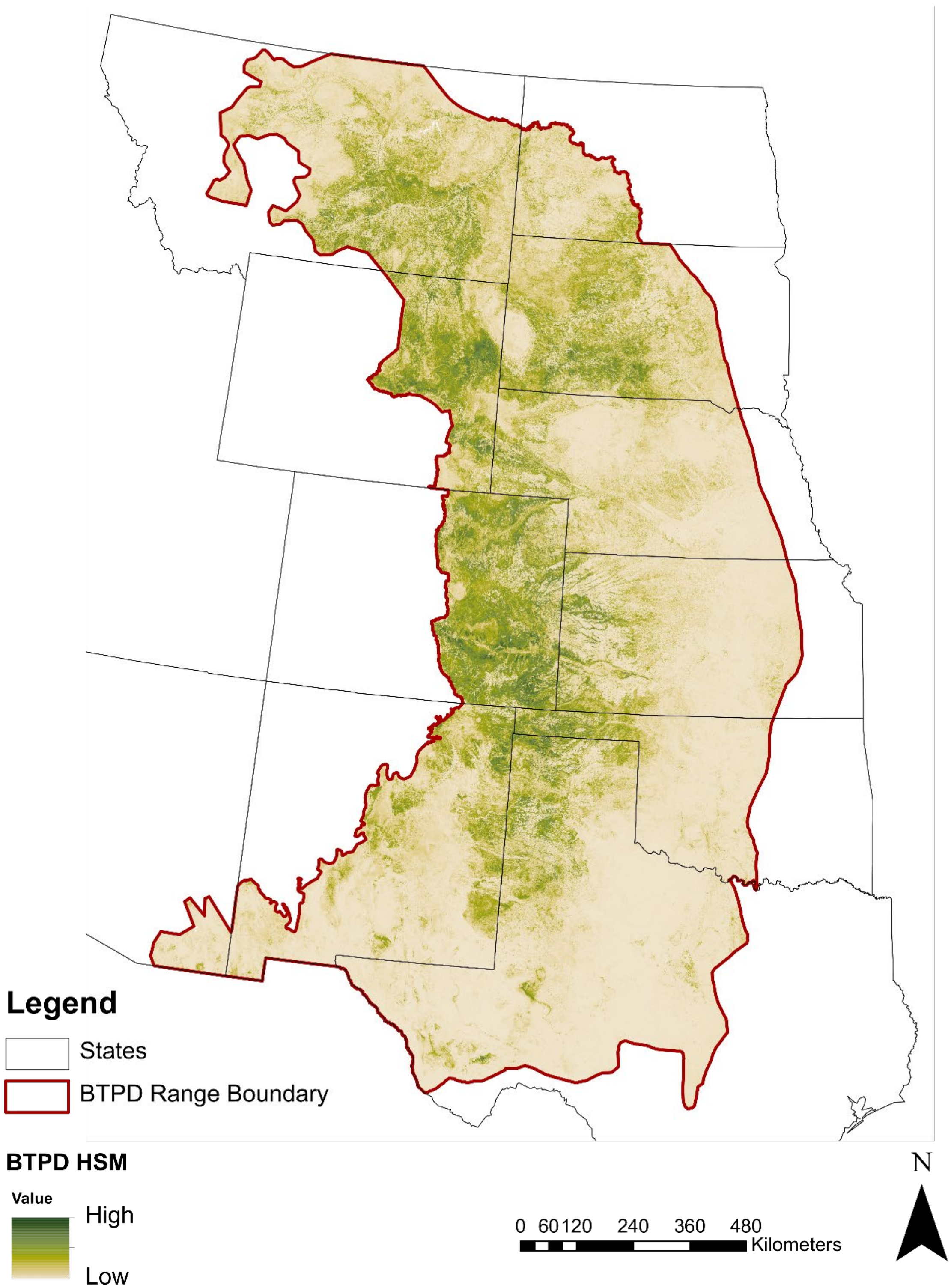

Fig. 5. *Black-tailed prairie dog (BTPD) ensemble habitat suitability model (HSM), under current climate. Dark green shows areas of highest habitat suitability for BTPDs, and beige shows areas of lowest suitability.*

Table 4. *Number of hectares of black-tailed prairie dog habitat that is of low, medium, and high suitability within each State and across the BTPD range.*

STATE NAME	Low	Medium	High
Montana	1,763,366	1,345,433	1,588,702
North Dakota	340,733	180,275	63,826
South Dakota	1,711,314	1,277,664	1,470,485
Wyoming	1,064,272	1,021,180	1,961,438
Nebraska	692,534	441,174	389,552
Colorado	1,338,636	1,558,562	4,216,600
Kansas	631,120	420,207	760,199
Arizona	13,750	5,789	108
Oklahoma	280,290	212,791	480,503
Texas	1,018,266	804,629	1,064,014
New Mexico	1,169,982	863,150	728,047
Entire US Range	10,024,502	8,130,936	12,723,491

Projecting suitable habitat into the future under both scenarios (warm and wet; hot and dry) shows the suitable habitat shifts northward (Fig. 6). Under the warm and wet scenario, eastern Colorado remains a stronghold, and suitable habitat expands across Wyoming, Montana, western North Dakota, South Dakota, western Nebraska, Kansas, and central Texas. Suitable habitat under this scenario retracts across the Southwest, with reductions especially in southern and eastern NM with the northeastern part of NM remaining as highly suitable habitat; it also declines somewhat across the TX-OK panhandle region. Under the more extreme hot and dry future scenario, suitable habitat substantially declines across the Southwest through Texas, Oklahoma and Kansas. Central and northeastern New Mexico and eastern Colorado remain favorable habitat but become the southern edge of suitable range, with the heart of suitable habitat projected to occur across Wyoming, Montana, and the Dakotas. We did not model the future scenarios beyond the known historical range within the United States, but it is likely suitable range could expand beyond the historical range in North Dakota, Montana, and Canada with the overall northward range shift.

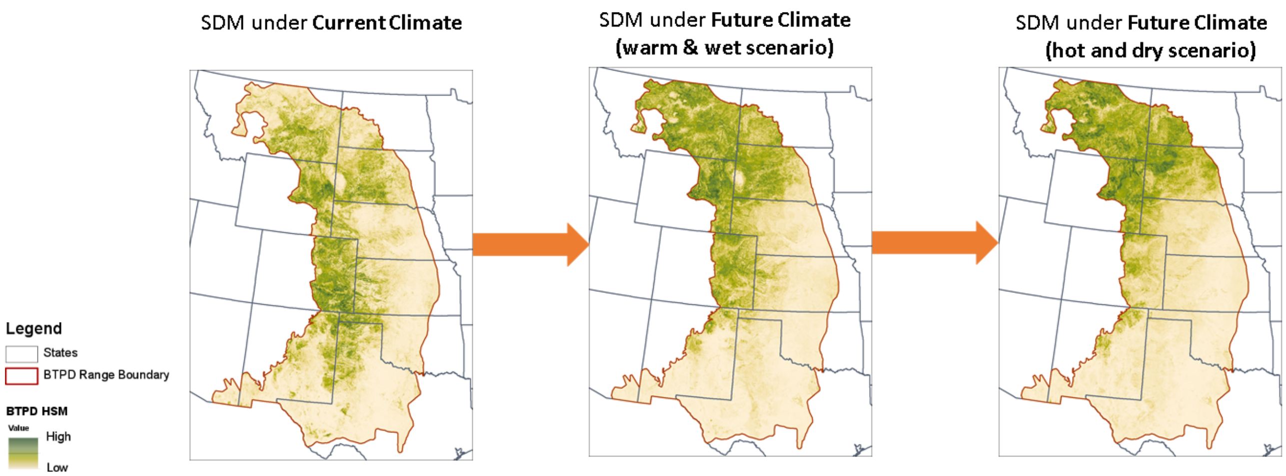

Fig. 6. *Black-tailed prairie dog (BTPD) habitat suitability models under current climate and future climate scenarios. Dark green shows areas of highest habitat suitability for BTPDs, and beige shows areas of lowest suitability.*

FINAL PRODUCTS:

The BTPD HSM maps for current and future climate are available now to partners upon request (Please contact Ana Davidson: ana.davidson@colostate.edu) but will not be made publicly available until results are published.

ACKNOWLEDGEMENTS

We thank Imtiaz Rangwala, Climate Science Lead, North Central Climate Adaptation Science Center for guidance on modelling habitat suitability for BTPDs under future climate. The MACA website provides this data acknowledgement statement for the future climate projections, "The dataset MACAv2-METDATA was produced with funding from the Regional Approaches to Climate Change (REACCH) project. We acknowledge the World Climate Research Programme's Working Group on Coupled Modeling, which is responsible for CMIP5, and we thank the climate modeling groups for producing and making available their model output. For CMIP5, the U.S. Department of Energy's Program for Climate Model Diagnosis and Intercomparison provides coordinating support and led development of software infrastructure in partnership with the Global Organization for Earth System Science Portals."

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SUPPLEMENTARY DOCS

Table S1. *Mean 10-fold Cross-Validation Performance metrics on the Testing dataset for the Generalized Linear Mixed-Model (GLMM), Random Forest model (RF), and Boosted Regression Trees model (BRT) when sensitivity = 95%.*

Model	AUC	TSS	err_rate	kappa	PCC	Sensitivity	Specificity	Threshold
GLMM	0.891	0.552	0.224	0.552	0.776	0.95	0.602	0.035
RF	0.970	0.788	0.106	0.788	0.894	0.95	0.838	0.232
BRT	0.922	0.624	0.188	0.624	0.812	0.95	0.674	0.165
Ensemble	0.956	0.734	0.133	0.734	0.867	0.95	0.784	0.206

Table S2. *Ensemble model metrics (against the Testing dataset) for when sensitivity = specificity, sensitivity = 95%, and specificity = 95%. Sensitivity (True Positive Rate); Specificity (False Negative Rate).*

	AUC	TSS	err_rate	kappa	PCC	Sensitivity	Specificity	Threshold
Sensitivity = Specificity	0.96	0.781	0.109	0.781	0.891	0.893	0.888	0.321
Sensitivity 95%	0.96	0.746	0.127	0.746	0.873	0.950	0.796	0.217
Specificity 95%	0.96	0.756	0.122	0.756	0.878	0.806	0.950	0.435

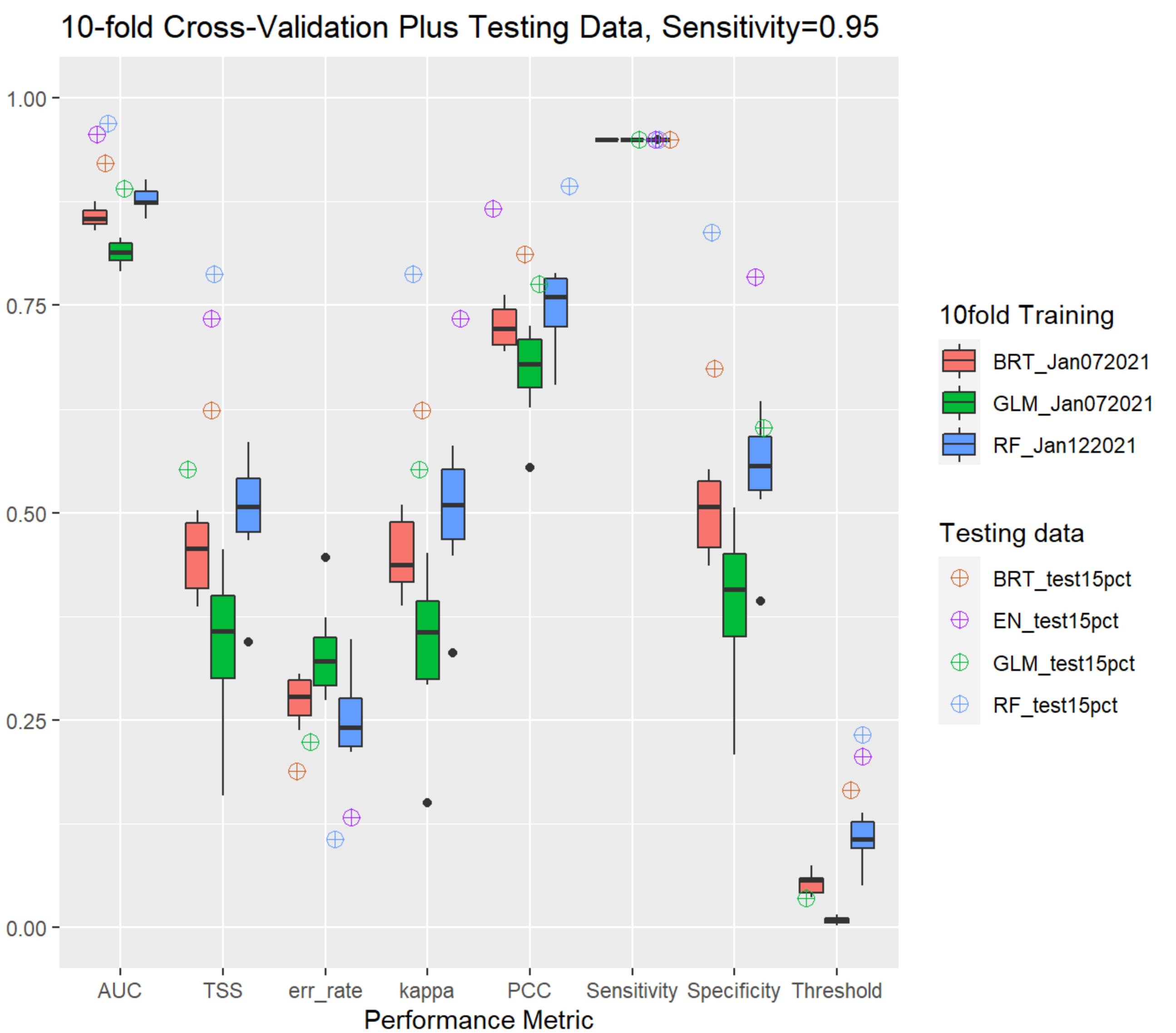

Figure S1. *Performance metrics of the 10-fold cross validation and tweaking dataset for the Generalized Linear Mixed-Model (GLMM), Random Forest model (RF), Boosted Regression Trees model (BRT), and Ensemble when sensitivity = 95%.*

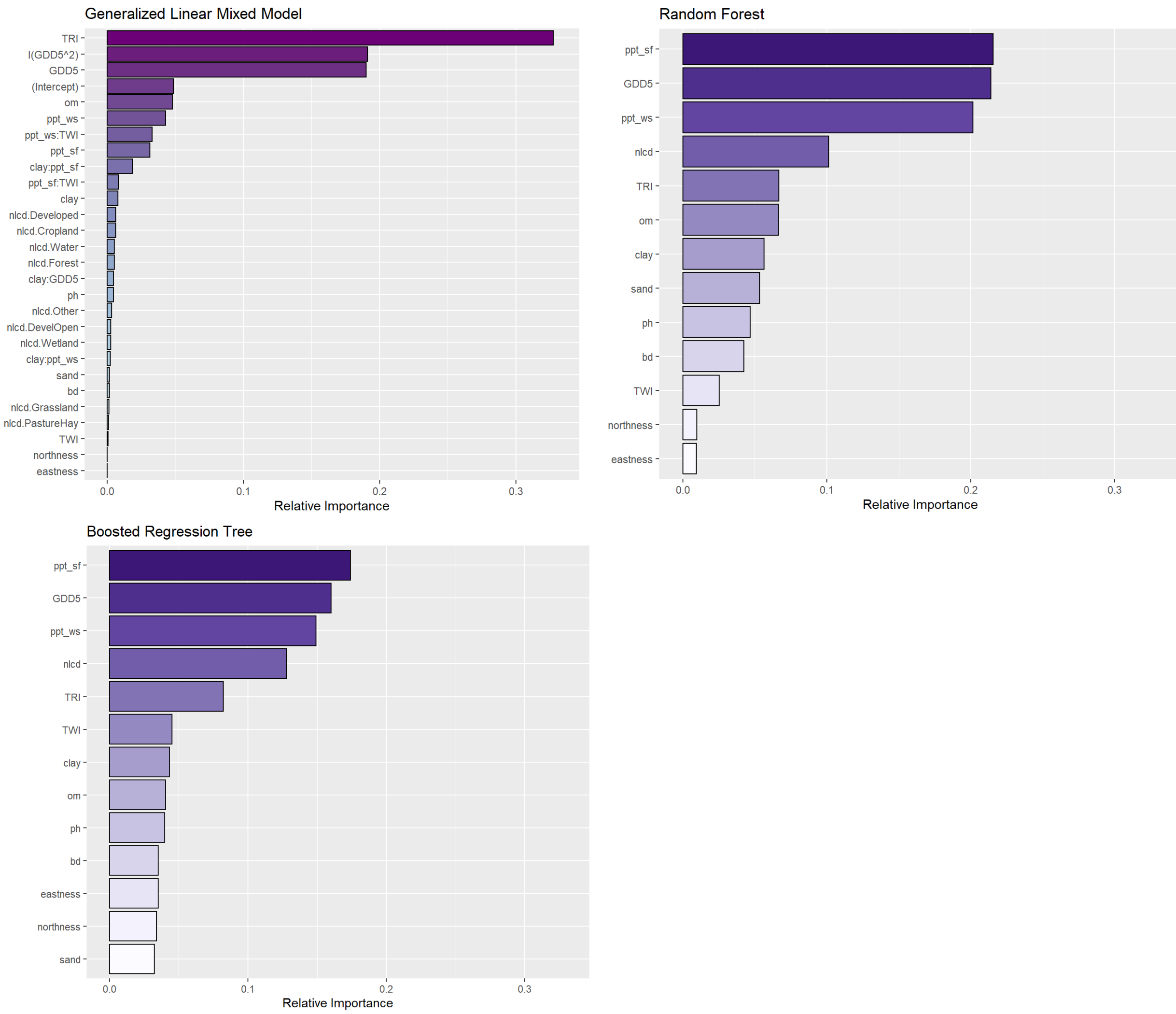

Figure S2. Variable importance plots for the Generalized Linear Mixed Model, Random Forest, and Boosted Regression Tree. All values have been normalized so that the sum of all variable importance measures for a model = 1.

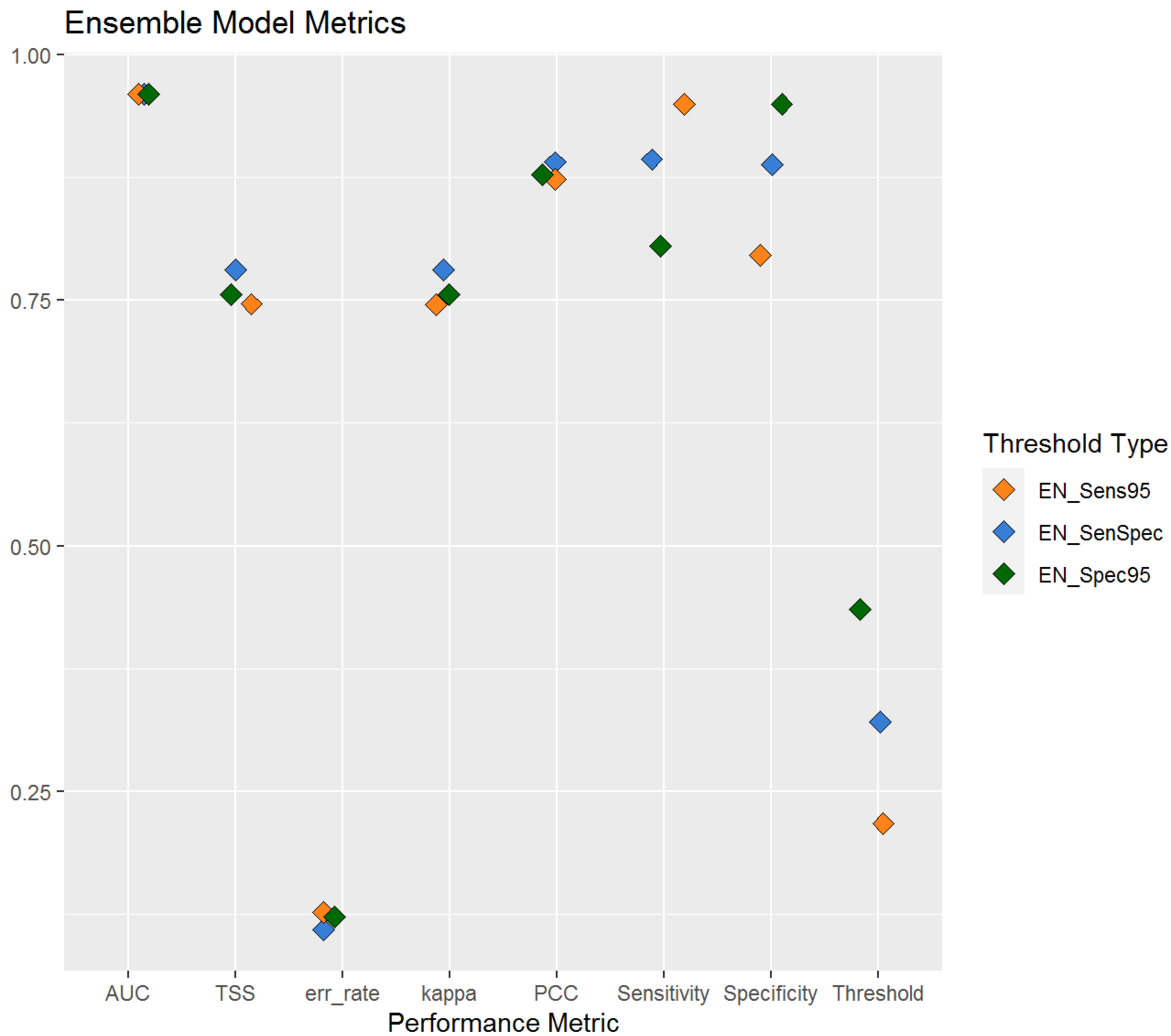

Fig. S3. *Ensemble model performance when sensitivity = specificity, sensitivity = 95%, and specificity = 95%. Sensitivity (True Positive Rate); Specificity (False Negative Rate).*

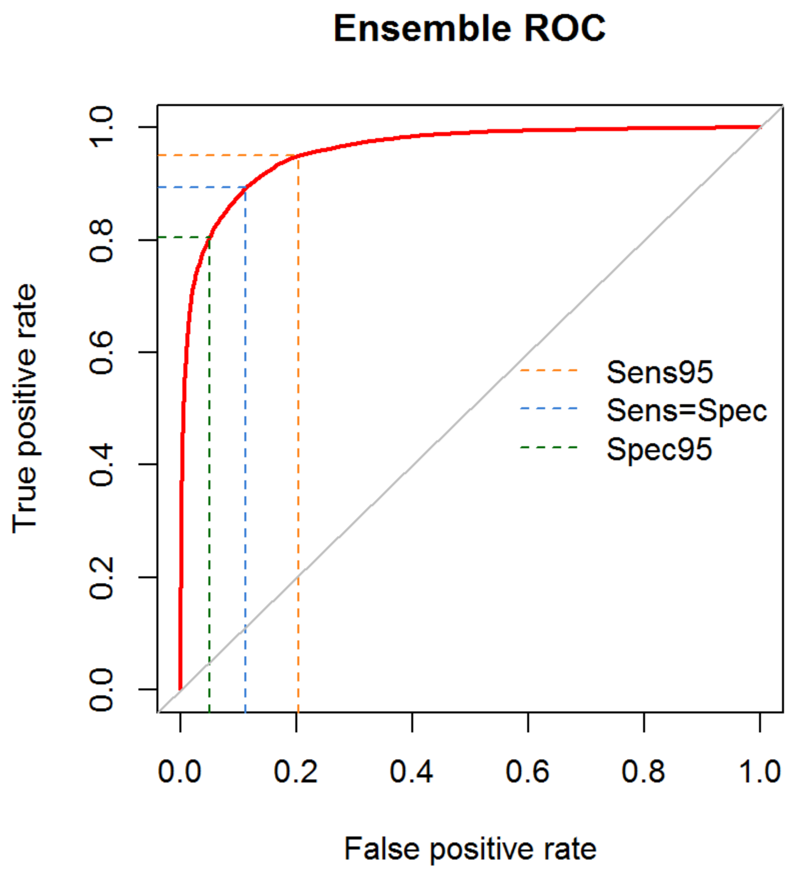

Fig. S4. *Ensemble model performance when sensitivity = specificity, sensitivity = 95%, and specificity = 95%. ROC curve shows relationship between sensitivity (true positive rate) and specificity (true negative rate). Gray solid line indicates random performance. Dashed lines show the values the axes measure for the thresholds at: Sensitivity = 0.95 (0.217); Sensitivity = Specificity (0.321); Specificity = 0.95 (0.435).*