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# Present and future suitable habitat for the black-tailed prairie dog ecosystem

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ABSTRACT

The black-tailed prairie dog (BTPD) ecosystem is an important component of North America's Central Grasslands, which are highly imperiled. Here, we develop a habitat suitability model (HSM) for the BTPD ecosystem across their historical geographic range within the United States to support conservation planning in the region. We used an ensemble HSM approach and spatial analysis combining ecological and climatic variables to quantify suitability of habitat for the black-tailed prairie dog ecosystem, both under today's current climate and projected into the future. We identified 20.8 million hectares of suitable grassland habitat for the black-tailed prairie dog ecosystem, indicating that large areas of quality habitat remain across the western half of their historic range. We also identified a significant northward expansion of their geographic range with future climate change scenarios, with a concomitant decline in habitat suitability across the southern Central Grasslands. Our results show that there is substantial conservation potential for the BTPD ecosystem, given the large amount of remaining available habitat, especially across the western portion of their historical range. Currently, however, we estimate that only ca. 1.9 million hectares (9 %) of this habitat are occupied by BTPDs. The recovery of the black-tailed prairie dog ecosystem is a complex, multidimensional, socio-ecological challenge. The maps we generated in this analysis provide the basis to carry out spatial analyses that also consider the social, political, and threat landscapes and to incorporate such findings into other large-scale, multi-species conservation planning efforts being developed for the Central Grasslands of North America.

## 1. Introduction

Temperate grasslands are the most imperiled and least protected of the world's terrestrial biomes (Bardgett et al., 2021; Carbutt et al., 2017; Jacobson et al., 2019). North America's Central Grasslands have undergone some of the greatest ongoing losses, transformed by agriculture, oil and gas development, desertification and woody plant encroachment, fencing, urbanization, and altered surface water distribution (Allred et al., 2015; Augustine et al., 2021; Morford et al., 2022; Olimb and Robinson, 2019; Van Auken, 2000; Weltzin et al., 1997). The abundance of wildlife that historically occurred across the Central Grasslands once rivaled Africa's Serengeti, but the pervasive anthropogenic impacts have resulted in widespread declines in grassland habitat and wildlife (Knowles et al., 2002; Lark et al., 2020; Samson et al., 2004; Sanderson et al., 2008). Awareness of the plight of the Central Grasslands has been increasing, especially over the last several years, with initiatives like the *Central Grasslands Roadmap*, *Great Plains Summit*, WAFWA's *Western Grasslands Initiative*, and introduction of *The North American Grasslands Conservation Act of 2022* to the U.S. Congress (Central Grasslands Roadmap [WWW Document], 2022; Comer et al., 2018; Finch, 2018; Haaland et al., 2021; Heady and Child, 2021; Lark et al., 2020; Western Association of Fish and Wildlife Agencies, 2011; Wyden, 2022). These efforts, and others, aim to focus limited conservation resources (Gary et al., 2022). One key approach centers on

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identifying species that serve as umbrellas for suites of other species, such as management focused on protecting the lesser prairie chicken (*Tympanuchus pallidicinctus*), which provides a conservation benefit for 84 % of other co-occurring at-risk species (Gary et al., 2022). The umbrella concept naturally extends to ecosystem engineers that play large and unique ecological roles, such that conservation efforts centered on them consequently encompass habitats they create and the species associated with them (Johnson et al., 2017).

The black-tailed prairie dog ecosystem is an important component of North America's Central Grasslands (Davidson et al., 2012; Hoogland, 2006). The prairie dog ecosystem is characterized by unique islands of open grassland habitat, dotted with burrow mounds, and occupied by a suite of associated species (Davidson et al., 2012; Whicker and Detling, 1988). The extensive burrow systems prairie dogs engineer provide critical refugia for a suite of invertebrates, amphibians, reptiles, birds and other mammals (Davidson et al., 2012; Whicker and Detling, 1988) and their colonies attract numerous species that prefer open grassland habitat that the prairie dogs meticulously maintain, such as burrowing owls (*Athene cunicularia*) and mountain plovers (*Charadrius montanus*) (Augustine and Baker, 2013; Augustine and Derner, 2012; Davidson et al., 2012; Duchardt et al., 2023). Pollinators also are 2–3 times more abundant on colonies than off because of the greater abundance of forbs and availability of oviposition sites (Hardwicke, 2006). Large herbivores, like bison (*Bison bison*) and cattle (*Bos taurus*), also are attracted to their colonies because of the more nutritious forage available compared to off colony (Bayless and Beier, 2011; Connell et al., 2019; Kotliar et al., 2006). Additionally, prairie dogs are an abundant and reliable source of prey for many predators including coyotes (*Canis latrans*), American badgers (*Taxidea taxus*), raptors [e.g., golden eagles (*Aquila chrysaetos*), ferruginous hawks (*Buteo regalis*)], and the highly endangered black-footed ferret (*Mustela nigripes*) (Davidson et al., 2012; Eads et al., 2016; Eads and Biggins, 2015; Goodrich and Buskirk, 1998; Grassel et al., 2015; Kotliar et al., 2006).

Prior to European settlement and the introduction of plague, prairie dog colony complexes were abundant across the Central Grasslands of North America, stretching from the northern plains in southern Canada to the desert grasslands of northern Mexico (Augustine et al., 2008a; Davidson et al., 2012; Eads and Biggins, 2015; Knowles et al., 2002; Kotliar et al., 2006). Through their burrowing and herbivory, prairie dogs transformed and shaped these grasslands, but today, their populations have declined by over 95 % across their range, along with consequent declines in associated species (Davidson et al., 2012; Hoogland, 2006). Once large, stable features across the grasslands, prairie dog colonies are now much smaller and highly unstable, largely due to widespread poisoning that began in the early 1900s and the introduction of plague, a non-native disease from Asia that causes collapses in populations of prairie dog and associated species (Augustine et al., 2008a, b; Davidson et al., 2022; Duchardt et al., 2023; Eads and Biggins, 2015; Livieri et al., 2022). Today, plague is probably the greatest threat to the prairie dog ecosystem across most of the BTPD range (Barrile et al., 2023; Cully et al., 2010; Eads and Biggins, 2015). Across the southern part of their range, increasing frequency and intensity of drought under a changing climate also is a significant threat in this region, causing declines in prairie dogs and associated species, and challenging restoration efforts (Avila-Flores et al., 2012; Davidson et al., 2014; Davidson et al., 2010; Facka et al., 2010). Analyses to assess how climate change could affect the broad-scale distribution of black-tailed prairie dogs are needed.

The USFWS identified "the single, most feasible action that would benefit black-footed ferret recovery is to improve prairie dog conservation" (U.S. Fish and Wildlife Service, 2013). Identifying where to focus conservation efforts for the prairie dog ecosystem requires understanding where the most ecologically suitable habitat is located and the broader landscape within which it is embedded (Crawford et al., 2020; Duflot et al., 2018; Gary et al., 2022; Olimb et al., 2022). Also critical for long-term conservation planning is understanding how areas that are identified as suitable habitat today might change in the future under a rapidly warming climate (Reside et al., 2018). Here, we develop the first range-wide habitat suitability model (HSM) for the black-tailed prairie dog ecosystem under both current and future climate to help inform conservation efforts for North America's Central Grasslands. Our HSM is based on presence and absence data for prairie dog occurrences across the geographic range of the BTPD within the United States, and quantifies how prairie dog occurrences relate to climate, soils, topography, and land cover. We also project the BTPD HSM under two future climate scenarios: 1) warm and wet and 2) hot and dry.

## 2. Methods

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 a consistent time period (McDonald et al., 2015). The WEST data are based on prairie dog colonies identified using National Agriculture Imagery Program (NAIP) imagery (1m$^2$ resolution) from a stratified random sample of 3.2 by 3.2 km grid cells distributed across the BTPD range within the United States (Table S1). We provide a brief overview here of the methods used by McDonald et al. (2015), but see report for full details. Two independent, trained observers visually and systematically searched each grid cell for prairie dog colonies at a scale of 1:4000. Observers identified colonies based on detection of burrow mounds, reduced vegetation height, "clip lines" around colony edges (indicating where vegetation had been clipped by prairie dogs), and vegetation texture that contrasted from off colony vegetation. Observers then digitized the boundaries of each colony and calculated their acreage across a sample of 20 % of the grid cells across Arizona, 1000 grid cells across each other state evaluated, and about 10 % of grid cells across lands managed by the Bureau of Land Management. Researchers adjusted their estimates for false negatives (missed colonies) by modeling the probability of detection of potential colonies. Range-wide estimates for colony acreage and number of colonies had coefficients of variation of 2.4 % and 4.9 %, respectively. To account for the higher level of sampling effort by McDonald et al. (2015) in Wyoming and Colorado, we subsampled grid cells in these two states in order to obtain an equal density of grid cells in each state across the BTPD geographic range.

We transformed the WEST data into a set of BTPD presence and absence points to make it suitable for data analyses. For each colony polygon detected within a given grid cell, we randomly selected one presence point per colony hectare. We 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 × 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 the HSM analysis.

Our BTPD range boundary is based on current and historical distribution. To determine current range, we largely followed the WEST (McDonald et al., 2015) boundary and extended the range boundary where appropriate to reflect the historical range distribution based on museum specimens. Each state's 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 the boundary were stored in the project database along with detailed metadata for each.

Next, we identified the most current spatial data layers available for soils, climate, topography, and land cover (Table 1 and Fig. 1). 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,

**Table 1**
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 (McDonald et al., 2015). |
| Land Cover | USGS National Land Cover Database 2016 (USGS, 2019). |
| Soils | POLARIS 30-m resolution database (Chaney et al., 2019a, b). Metrics: bulk density to 100 cm, Sand to 100 cm, %Clay to 100 cm, % organic matter to 100 cm, pH to 100 cm. |
| Slope & elevation | National Elevation Dataset (USGS, 2018). Metrics: Topographic Wetness Index, Topographic Ruggedness Index, slope, aspect. |
| Climate – current | Current climate (1994–2014), using gridMet (Abatzoglou, 2013). 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 (Abatzoglou and Brown, 2012; "MACAv2 METDATA"). Metrics: Mean annual precipitation (mm), winter + spring & summer + fall precipitation, max summer temperature, potential evapotranspiration, growing degree days. |

based on the data sources in Table 1. First, we used the 2016 National Land Cover Database (NLCD), which was released by USGS in May of 2019. This 2016 database represents a major improvement from the 2011 NLCD, 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 U.S., POLARIS (Chaney et al., 2019a, b), that builds upon SSURRGO. It includes improved interpolation of soil texture and other attributes down to a 30-m pixel resolution. One limitation is that this improved soil model did not include depth to bedrock, which is an important factor influencing BTPD burrowing. We attempted to use the latest SSURGO soils data (Soil Survey Staff, 2016) 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 (Chaney et al., 2019a, b) 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; USGS, 2018) was likewise downloaded as individual 1-degree tiles and merged over the study area. We 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 (Tarboton, 2015) to calculate a Topographic Wetness Index and a Terrain Ruggedness Index at a 30 × 30 m pixel resolution for the entire BTPD range. The NED was also used to create information on aspect as a function of 'northness' and 'eastness'. We used the 2016 NLCD (USGS, 2019) to classify each pixel as one of 10 land cover categories (cropland, developed, developed open space, forest, grassland, shrubland, pasture/hay, water, wetland, and other), with shrubland used as the reference category in all models. We also used the NLCD to calculate 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 (Abatzoglou, 2013) 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. We used one-hot encoding to convert categorical data (primarily land cover) 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

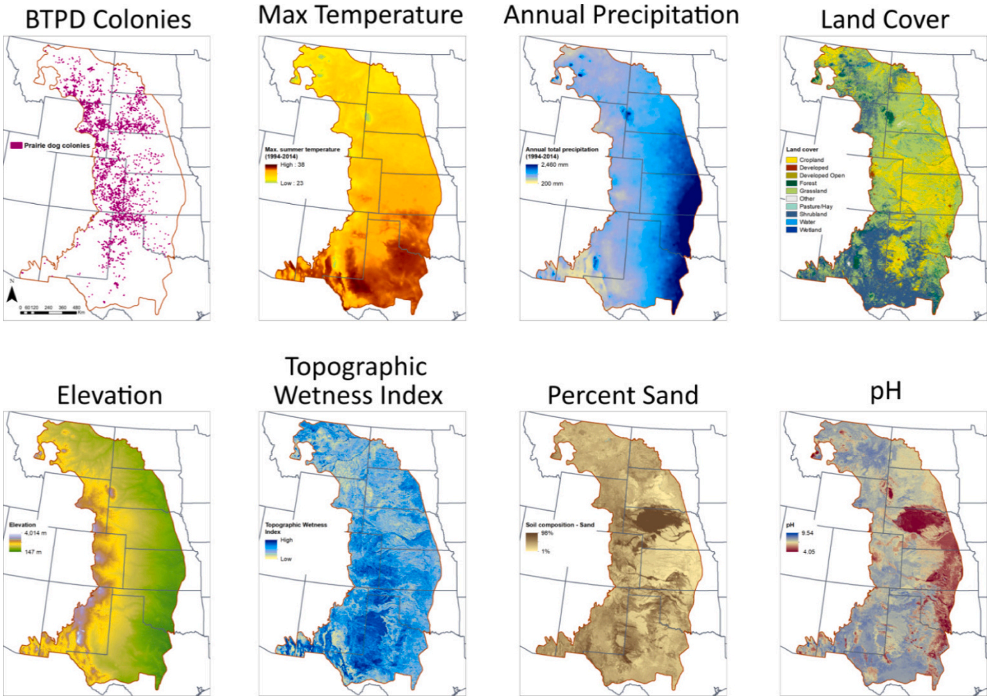


**Fig. 1.** Some of the spatial layers created for the black-tailed prairie dog (BTPD) habitat suitability model, based on BTPD occurrence (McDonald et al., 2015), climate (Abatzoglou, 2013), land cover (USGS, 2019), topography (USGS, 2018), and soils (Chaney et al., 2019a, b).

**Table 2**
Post-hoc analysis of the percentage of ground-truthed and ground-mapped black-tailed prairie dog colonies that occurred within habitat that was predicted to be low, medium, or high suitability. Last row of table shows total occupied area (ha) across all ground-truthed and ground-mapped colonies and for each site. Over 92 % of all ground-truthed and ground-mapped colonies fell into habitat that was predicted to be of medium or high suitability, based on a weighted average of occupied colony area at each site.

| Habitat Suitability | ALL Colonies | Kiowa NG, New Mexico | Vermejo Park Ranch, New Mexico | State of Colorado | Pawnee NG, Colorado | Comanche NG, Colorado | Thunder Basin NG, Wyoming | Rita Blanca NG, Texas & Oklahoma | Cimmaron NG, Kansas | Oglala NG, Nebraska | Conata Basin, South Dakota | Bad River Ranch, South Dakota | American Prairie, Montana |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Low | 7.48 % | 0.80 % | 25.97 % | 3.46 % | 3.22 % | 15.85 % | 0.89 % | 1.74 % | 2.67 % | 6.05 % | 7.39 % | 14.14 % | 22.51 % |
| Medium | 15.68 % | 13.60 % | 27.42 % | 9.98 % | 26.24 % | 19.57 % | 6.16 % | 19.08 % | 7.66 % | 50.33 % | 14.24 % | 46.62 % | 61.80 % |
| High | 76.66 % | 85.58 % | 46.61 % | 86.56 % | 70.54 % | 64.59 % | 92.94 % | 79.18 % | 89.67 % | 43.61 % | 78.37 % | 39.24 % | 15.68 % |
| Medium + high | 92.52 % | 99.18 % | 74.03 % | 96.54 % | 96.78 % | 84.16 % | 99.10 % | 98.26 % | 97.33 % | 93.94 % | 92.61 % | 85.86 % | 77.48 % |
| Area (ha) | 63,298 | 864 | 4114 | 13,987 | 1892 | 8622 | 11,767 | 3057 | 2249 | 857 | 14,313 | 974 | 1560 |

modeling, we narrowed down environmental inputs based on covariate correlation, proportion of deviance explained, and effect on model performance (Table S2). We dropped 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.

To determine the best-fit habitat suitability model for our data, we evaluated the performance of several different independent models and an ensemble model (Araújo et al., 2019; Guisan et al., 2017). Specifically, we created BTPD habitat suitability models using: 1) Generalized Linear Mixed Models (GLMM), 2) Random Forest models (RF), 3) Boosted Regression Trees models (BRT, also known as Generalized Boosted Models or GBM), and 4) an ensemble model that combined the outputs of the GLMM, RF, and BRT0. HSMs. Models were created using the R packages *lme4* (Bates et al., 2015), *randomForest* (Liaw and Wiener, 2002), and *dismo* (Hijmans et al., 2017). The GLMM used the identity of the 3.2 × 3.2 km 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.

For model training, we randomly selected 70 % of the 3.2 × 3.2 km grid cells sampled by McDonald et al. (2015), and used the presence and absence points within them. This approach maintained equal numbers of presence and absence points in the training dataset. 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 four final models (Table S3, 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 for model fitting 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 were calculated by averaging six performance metrics [Area under the Curve (AUC), True Skills Statistic (TSS), Percent Correctly Classified (PCC), kappa, Sensitivity, and Specificity], which were themselves averaged over a 10-fold cross-validation of the models built on the Training dataset. This gave 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 S3).

We also conducted a post-hoc analysis of the percentage of predicted suitable habitat of low, medium, and high quality that fell within colonies that were ground-truthed and/or ground-mapped across the BTPD range (Table 2). These colonies were not used to train our model, so provide complementary insight into the accuracy of our HSM. The colonies in this dataset were mapped: across the state of Colorado (2016); Vermejo Park Ranch, NM (2017); Bad River Ranch, SD (2010); American Prairie, MT (2020); Cimarron National Grassland (NG), KS (2004); Comanche NG, CO (2014); Rita Blanca NG, TX and OK (2014); Kiowa NG, NM (2004); Conata Basin, SD (2007); Thunder Basin NG, WY (2014); Oglala NG, NE (2010); Pawnee NG, CO (2011). If multiple years of colony data were available at a given site, we selected a year (shown in parentheses above) when colony areas were at their larger extents, but not necessarily at their largest (peak). We did this to capture the greater area that prairie dogs will utilize, while not necessarily the lower quality habitat they are more likely to expand into during peak years. We defined three classes of habitat suitability (low, medium, and high). Specifying how different probability values predicted by the ensemble model correspond to classes of suitable versus unsuitable habitat depends upon the level and types of error that one is willing to accept. Given the design of our sampling, where locations of BTPD colonies represent used habitat and locations lacking BTPD colonies represent available habitat, the "available" habitat is likely to include both areas of high quality (or potentially suitable) habitat that has not yet been colonized, and areas of low quality (or unsuitable) habitat that is being avoided by colonizing prairie dogs. In this view, false negative model predictions (i.e., where pixels occurring within known BTPD colony locations are predicted to not have BTPDs present) are a more egregious error than false positive model predictions (i.e., where pixels within "available" habitat are predicted to have BTPD present). We therefore defined "low quality habitat" as those pixels where the probability values predicted by the ensemble model were below the cutoff for a 5 % false negative rate. In contrast, we define "high quality habitat" as areas where probabilities predicted by the ensemble model were above the cutoff associated with a 5 % false positive rate. Medium quality habitat was defined as areas with probabilities in between these two cutoff values.

### 2.1. *BTPD habitat suitability model under future climate*

Next, we projected our BTPD HSM into the future (2100) under two different climate scenarios: 1) warm and wet (IPSL-CM5A-LR_r1i1p1_rcp45); and 2) hot and dry (MIROC5_r1i1p1_rcp85). These climate scenarios were selected because they represent two different ends of the spectrum for scenarios across our study region. The future climate model scenarios were obtained from MACAv2_METDATA [WWW Document], 2020, and were averaged over 2076–2099 (Table S2). 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., 2012) utilizing the Multivariate Adaptive Constructed Analogs (MACA; Abatzoglou and Brown, 2012) method with the METDATA (Abatzoglou, 2013) observational dataset as training data."

### 2.2. *Ensemble model review*

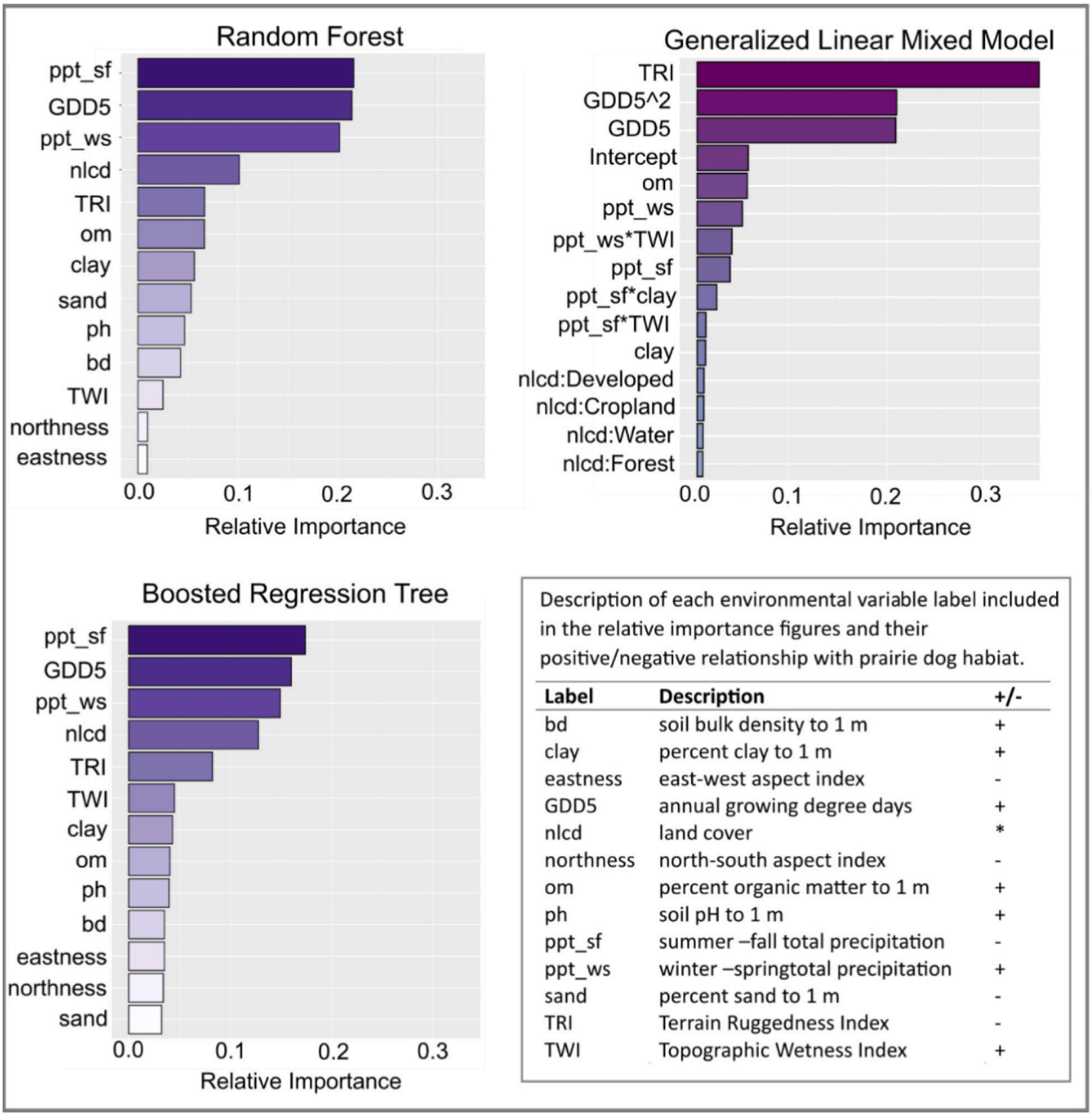
During summer 2020, our team met with biologists from each state individually and with other experts on the prairie dog ecosystem to provide detailed state-level review of the ensemble habitat suitability map. After extensive review, our team worked to address each of the comments we received. One challenge was modeling the desert grasslands of the American Southwest (Arizona, southern New Mexico, southwestern Texas), where prairie dogs occurred historically, and considerable grassland remains. 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 (Davidson et al., 2018; Davidson et al., 2014; Facka et al., 2010; Hale et al., 2013). Nevertheless, extensive grassland remains in the region and colonies do exist, just not in high enough abundance to be well-sampled by McDonald et al. (2015). To address this, we obtained additional, recent data (within the last ca. 10 years) for Arizona, New Mexico, and Texas from within the desert grassland ecoregion (The Nature Conservancy, 2008) 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 data and traded them out with the new grid cells ($N = 12$) covering the additional occurrence data. Thus, the dataset retained the same density of grid samples within each state. We also removed false positives in occurrence data identified during the reviews by biologists in each state. 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 BTPDs, based on consultation with the New Mexico Department of Game and Fish and the New Mexico Natural Heritage Program.

## 3. Results

Among the three models used to build the ensemble, the GLMM was more restrictive in identifying suitable prairie dog habitat compared to the RF and BRT models. But, the GLMM performed better at modeling suitability relative to soils across the BTPD range compared to the RF and BRT, while RF and BRT modeled suitability relative to climate better than GLMM. Climate variables were important predictors across all models, followed by topography and landcover (Fig. 2). For the final selected GLMM, the variables of greatest importance were topographic ruggedness, growing degree days, land cover type, soil texture (% clay and % sand), soil organic matter and soil pH (see Table S4 for coefficients). 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. 2). Across all models, predicted habitat suitability was maximized at intermediate values for growing degree days (i.e., intermediate levels of net primary productivity), increased with more winter-spring precipitation, and declined with more summer-fall precipitation. Habitat suitability was strongly positive for grassland, strongly negative for cropland, developed land, forests and water, and weakly negative for developed open space and wetlands. BTPD habitat suitability was positively associated with increased soil clay content, organic matter content and pH, and negatively associated with topographic ruggedness and soil sand content.

When we compared performance metrics of all four models (GLMM, RF, BRT, ensemble), the RF model performed slightly better than the ensemble, followed by BRT and GLMM (Table S3; Fig. S1). However, we selected the ensemble model to build our HSM because not only did it perform similarly well to the RF, but the ensemble HSM also reduced the impact of individual model biases. Indeed, ensemble HSMs often perform better than single HSMs because they can average out uncertainties and biases inherent in different model algorithms (Hao et al., 2019). 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 %, Specificity (ability to correctly classify non-prairie dog habitat) of 80 %, TSS of 0.75, kappa of 0.75, and PCC of 0.87 (Fig. 3). We also evaluated the model when Sensitivity was equal to Specificity and when Specificity was 95 % and found similar model performance (Table S5; Figs. S2 and S3). Our post-hoc analysis showed that 93 % of all ground-truthed and ground-mapped colonies were located in medium to high suitability habitat (Table 2; Fig. 4).

Based on the total area of colonies in each state estimated from McDonald et al.'s (2015) analysis of NAIP imagery, 90.7 % of medium or high suitability habitat for the prairie dog ecosystem was unoccupied by prairie dogs within their U.S. range, and a similar amount of quality habitat was unoccupied within each state (87–99.5 %; Table 3). 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, Wyoming, and Montana (Fig. 3). Under current conditions, the region containing the most extensive and contiguous patches of suitable habitat for BTPDs occurs in the nine counties of southeastern Colorado (Baca, Las Animas, Huerfano, Pueblo, Crowley, Otero, Bent, Prowers and Kiowa), which encompass 4.2 million ha (10.4 million ac) within the historic BTPD range. Within this region, we identified 2.6 million ha of moderate or high-quality BTPD habitat, primarily on gently undulating shortgrass plains. These plains are occasionally dissected by unsuitable or low-quality habitat associated with rugged canyonlands along the Purgatoire River and floodplains or cropland along the Arkansas River. The region is bounded on the south by mesas and canyonlands along the New Mexico/Oklahoma borders, and on the east by rowcrop agriculture near the Kansas border. Of the medium to high-quality habitat occurring in this region, 150,840 ha or 5.75 % is on the Comanche National Grassland and 78,802 ha or 3.0 % is on lands managed by the Department of Defense for military training. A second region of large and contiguous patches of suitable BTPD habitat persists in six counties of northeast Wyoming (Natrona, Converse, Niobrara, Johnson, Campbell and



Description of each environmental variable label included in the relative importance figures and their positive/negative relationship with prairie dog habiat.

| Label | Description | +/- |
|---|---|---|
| bd | soil bulk density to 1 m | + |
| clay | percent clay to 1 m | + |
| eastness | east-west aspect index | - |
| GDD5 | annual growing degree days | + |
| nlcd | land cover | * |
| northness | north-south aspect index | - |
| om | percent organic matter to 1 m | + |
| ph | soil pH to 1 m | + |
| ppt_sf | summer –fall total precipitation | - |
| ppt_ws | winter –springtotal precipitation | + |
| sand | percent sand to 1 m | - |
| TRI | Terrain Ruggedness Index | - |
| TWI | Topographic Wetness Index | + |

**Fig. 2.** Variable importance plots for the Random Forest, Generalized Linear Mixed Model, and Boosted Regression Tree. All values have been normalized so that the sum of all variable importance measures for a model = 1. See Table S2 for complete details of each variable. *Note that Land cover was a categorical variable, with grassland cover having a positive relationship with prairie dog habitat and others (cropland, developed, wetland, wetland, forest) having a negative relationship. Additionally, in the GLMM ppt_ws*TWI and ppt_sf*clay had a negative relationship with prairie dog habitat; whereas ppt_sf*TWI had a positive relationship; see Table S4 for details.

Weston), which encompass 5.7 million ha (14.2 million ac) within the historic BTPD range. Within this region of Wyoming, we identified 2.4 million ha of moderate or high-quality BTPD habitat, with the largest expanse occurring on broad, flat plains immediately west of the Black Hills in Weston County. Of the medium to high-quality habitat occurring in this region, 139,953 ha or 5.9 % is on the Thunder Basin National Grassland.

Other notably extensive and contiguous regions of BTPD habitat occur in South Dakota associated with the Buffalo Gap National Grassland, Badlands National Park, and the Pine Ridge, Cheyenne and Standing Rock Indian Reservations, and in northeast Colorado surrounding the Pawnee National Grassland, and in Montana in the portions of Yellowstone, Treasure, and Rosebud counties north of the Yellowstone River. Suitable habitat also extends into the westernmost counties of Kansas and Nebraska, and into northeastern New Mexico (Fig. 3). 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.

Projecting suitable habitat into the future under both future scenarios (warm and wet; hot and dry) shows how suitable habitat shifts northward (Fig. 5). 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,

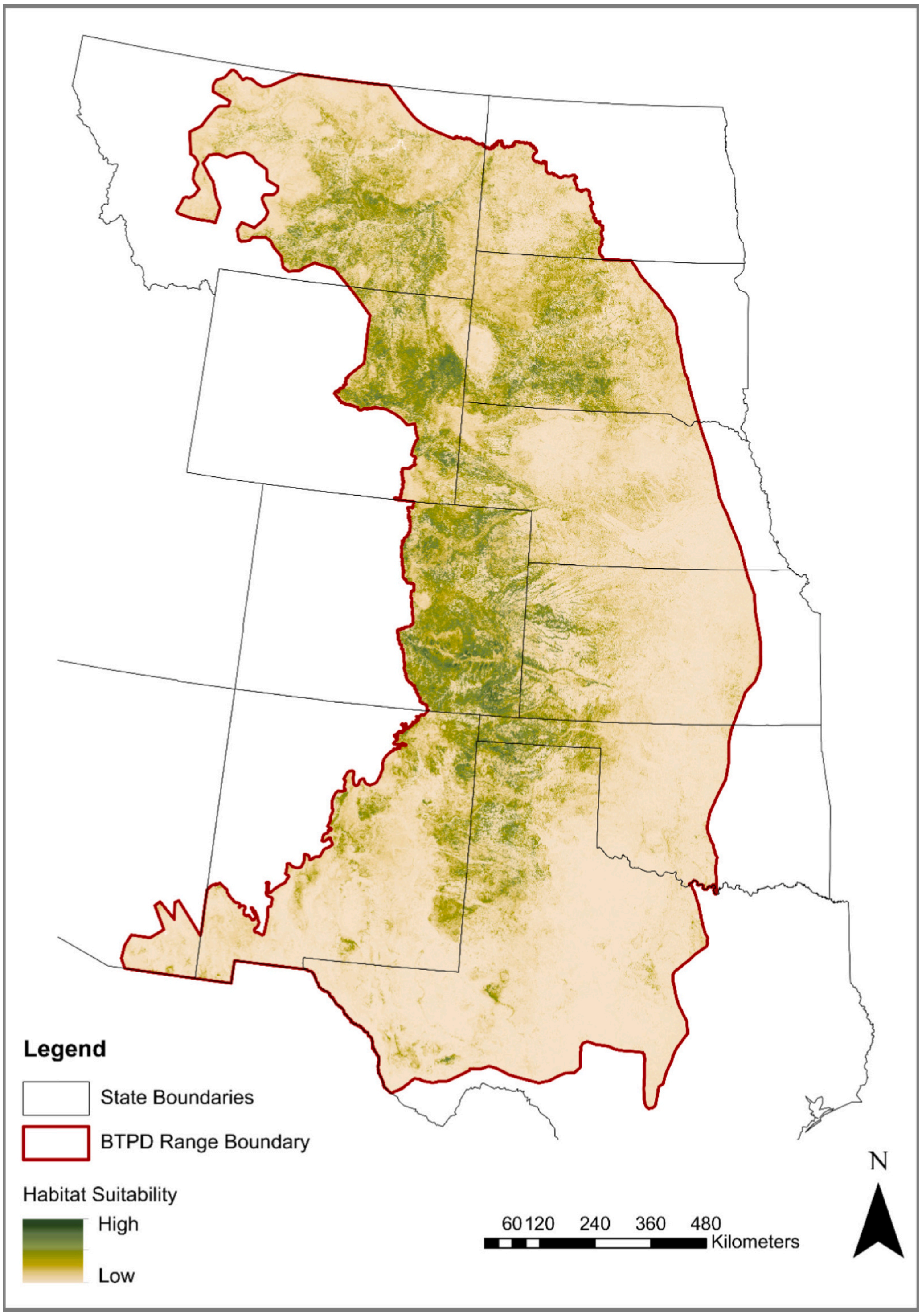


**FIG. 3.** Black-tailed prairie dog (BTPD) ensemble habitat suitability model, under current climate. Dark green shows areas of highest habitat suitability for BTPDs, and beige shows areas of lowest suitability. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Kansas, and central Texas. Suitable habitat under this scenario retracts across the Southwest, with reductions especially in southern and eastern New Mexico with the northeastern part of New Mexico remaining as highly suitable habitat. Suitability also declines somewhat across the Texas-Oklahoma 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 that suitable habitat could expand beyond the historical range in North Dakota, Montana, and Canada with the projected northward and eastward range shift.

## 4. Discussion

Our research shows there are large areas of suitable habitat available

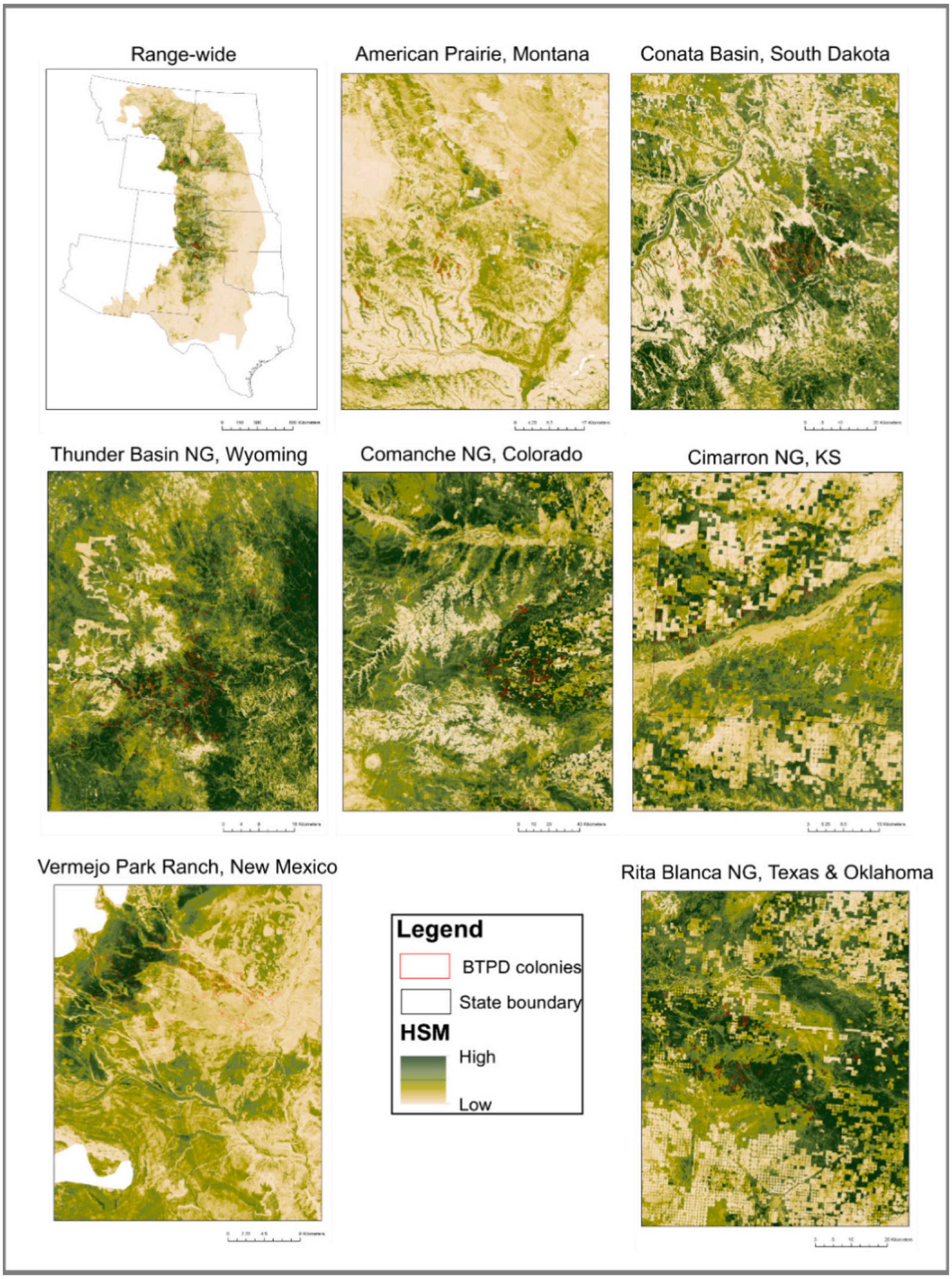


**Fig. 4.** Ground-truthed and ground-mapped black-tailed prairie dog (BTPD) colonies across Private Conservation Lands, the state of Colorado, and National Grasslands (NG), overlapped with BTPD ensemble habitat suitability model under current climate.

for the BTPD ecosystem, across their U.S. range and within each state. We identify 20.8 million hectares of remaining suitable grassland habitat. However, only 1.9 million hectares (9 %) are currently occupied by BTPDs. These results demonstrate the large amount of conservation potential for the prairie dog ecosystem. Such findings are especially encouraging for associated species that depend on BTPDs and their colonies for habitat, and for those species that require large colonies to support their populations (Augustine and Baker, 2013; Augustine and Skagen, 2014; Davidson et al., 2012; Duchardt et al., 2020; Livieri et al., 2022; U.S. Fish and Wildlife Service, 2013). Further, our HSM can help inform conservation planning and efforts to promote coexistence. For example, the impacts BTPDs can have on livestock producers (Crow et al., 2022; Vermeire et al., 2004) and the susceptibility of BTPD populations to plague (Cully et al., 2010; Davidson et al., 2022; Eads and Biggins, 2015) will continue to be major factors affecting conservation efforts for BTPDs. Mitigating impacts on livestock producers will require careful consideration of the spatial distribution of colonies on and adjacent to livestock operations, and how management can effectively maintain colony complexes in desired locations while preventing expansion into undesired areas. Our HSM can assist in planning efforts not only by ensuring that locations targeted for BTPD conservation are in optimal habitat, but also in identifying transition zones between high and low habitat suitability where expansion may be more effectively and naturally prevented, to reduce the need for lethal control. Our maps can

**Table 3**
Number of hectares of black-tailed prairie dog (BTPD) habitat that is of low, medium, high, and medium + high suitability within each state and across the BTPD range within the United States. Table includes estimated number of hectares occupied by BTPD colonies within each state based on WEST data (McDonald et al., 2015); the occupied area was corrected for false negatives (but not false positives) across all states except Wyoming (see Part 2 of McDonald 2015 report, Wyoming).

| State name | Area of low habitat suitability (ha) | Area of medium habitat suitability (ha) | Area of high habitat suitability (ha) | Area of medium + high habitat suitability (ha) | Area of medium + high habitat suitability occupied by BTPDs (ha) | Percent of medium + high habitat suitability occupied by BTPDs (%) |
|---|---|---|---|---|---|---|
| Arizona | 13,750 | 5789 | 108 | 5897 | 34 | 0.58 % |
| Colorado | 1,338,636 | 1,558,562 | 4,216,600 | 5,775,162 | 532,251 | 9.22 % |
| Kansas | 631,120 | 420,207 | 760,199 | 1,180,406 | 154,775 | 13.11 % |
| Montana | 1,763,366 | 1,345,433 | 1,588,702 | 2,934,135 | 184,055 | 6.27 % |
| Nebraska | 692,534 | 441,174 | 389,552 | 830,726 | 89,208 | 10.74 % |
| New Mexico | 1,169,982 | 863,150 | 728,047 | 1,591,197 | 124,098 | 7.80 % |
| North Dakota | 340,733 | 180,275 | 63,826 | 244,101 | 15,561 | 6.37 % |
| Oklahoma | 280,290 | 212,791 | 480,503 | 693,294 | 81,224 | 11.72 % |
| South Dakota | 1,711,314 | 1,277,664 | 1,470,485 | 2,748,149 | 224,145 | 8.16 % |
| Texas | 1,018,266 | 804,629 | 1,064,014 | 1,868,643 | 238,871 | 12.78 % |
| Wyoming | 1,064,272 | 1,021,180 | 1,961,438 | 2,982,618 | 288,606 | 9.68 % |
| Entire U.S. Range | 10,024,502 | 8,130,936 | 12,723,491 | 20,854,427 | 1,932,826 | 9.27 % |

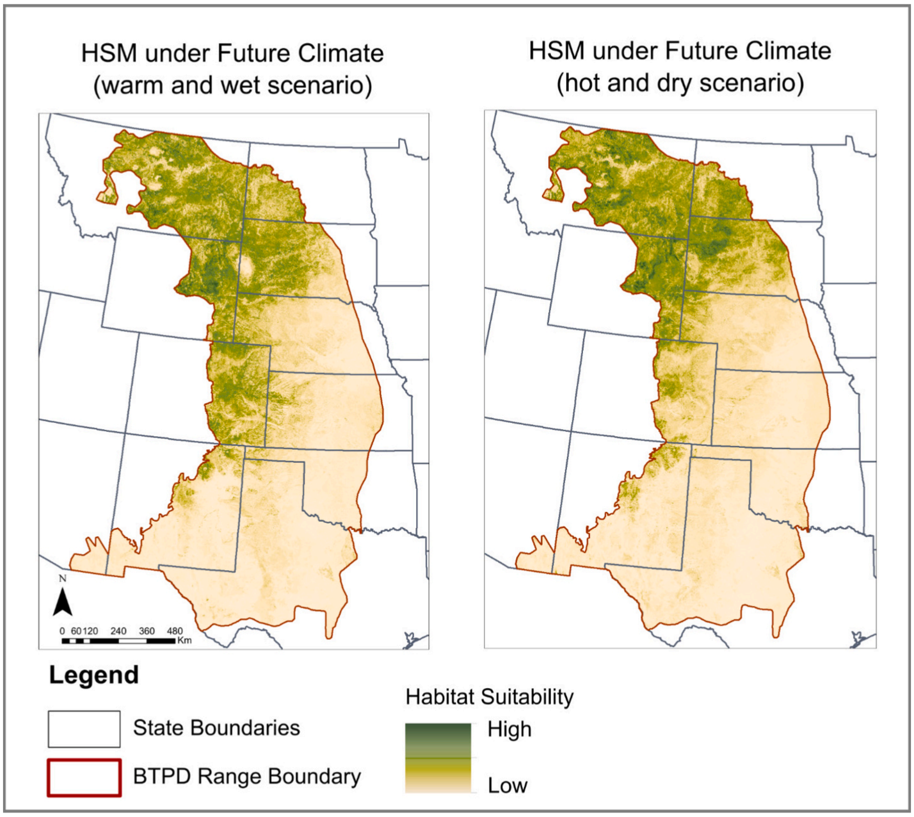


**Fig. 5.** Black-tailed prairie dog (BTPD) ensemble habitat suitability model (HSM) projected under future climate scenarios. Dark green shows areas of highest habitat suitability for BTPDs, and beige shows areas of lowest suitability. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

also be used to assess whether landscapes targeted for conservation efforts are large enough to support conservation goals for associated species such as BFFs and mountain plovers, which rely on extensive colony complexes (Augustine and Skagen, 2014; Dinsmore and Knopf, 2005; Duchardt et al., 2020). Additionally, the maps can support analyses of potential connectivity among colonies across landscapes, which often affects the likelihood and scale of plague epizootics (Barrile et al., 2023; Collinge et al., 2005; Davidson et al., 2022; Johnson et al., 2011). Another utility of our model could be informing which landowners might be best to participate in payment programs for BFF recovery (NRCS, 2022), by showing how their lands relate to the broader landscape and may help to achieve range-wide conservation goals.

Suitable habitat for the BTPD ecosystem shows a dramatic shift northward under both future climate scenarios in our analysis, which is consistent with climate projections for the Great Plains and consequent species' range shifts across the region and globally (Bradford et al., 2020; Chen et al., 2011; Roberts et al., 2019). Harsh winters are known to negatively impact prairie dog reproduction (Grassel et al., 2016; Stephens et al., 2018); milder winter conditions in the northern regions under a warming climate could have a positive impact on prairie dog populations. Given the northward trend, and projected expansion of C4 grasses across the northern plains (Klemm et al., 2020), we suspect suitable habitat will eventually extend beyond the current northern range boundary. Understanding this northward expansion would be worthy of future research. Meanwhile, there already have been significant losses in large prairie dog colony complexes in the southern portion of the BTPD range, not only due to plague, but also to increasing intensity and frequency of drought under climate change (Ceballos et al., 2010; Davidson et al., 2018; Davidson et al., 2014; Facka et al., 2010; Hale et al., 2013; Hayes et al., 2016), and our models indicate that recovery of these populations may be limited by climate change. Drought can suppress reproduction and population growth rates causing colony contractions and local extinctions (Davidson et al., 2014; Facka et al., 2010; Grassel et al., 2016; Hale et al., 2013; Hayes et al., 2016; Hoogland, 1995; Stephens et al., 2018). Nevertheless, our analysis highlights regions in the southern part of the range, such as northeastern New Mexico, that may remain suitable well into the future and be worthy of conservation investment, in addition to areas farther north (especially in Wyoming, Montana, and South Dakota).

Although we highlight a northward shift in suitable habitat for the BTPD ecosystem, we do not consider how climate change might interact with plague. When dry conditions are followed by wet weather with mild temperatures, the consequent increases in prairie dog densities, flea loads, and above-ground activity can coincide with conditions favoring fleas and plague transmission (Eads and Biggins, 2017). This suggests that the frequency of plague epizootics might increase where these conditions occur under a warming climate (Eads and Hoogland, 2017), which may become more typical across the northern region of their projected range (Fig. 5). Alternatively, Snäll et al. (2009) modeled future plague and black-tailed prairie dog dynamics under different climate change scenarios and found that plague may in fact decrease in the future, especially under those scenarios that project the greatest warming. They suggest the underlying mechanism reducing plague events is the effect of high temperatures on fleas and plague transmission. Understanding the role of climate in driving plague epizootics and how climate change might alter plague dynamics across the prairie dog range remains an important area of research (Barrile et al., 2023).

Our HSM highlighted climate, topography, and landcover type being the most important variables predicting suitable habitat for the BTPD ecosystem, with climate (growing degree days and precipitation) being the most important overall. Previous maps of BTPD habitat suitability developed for the southern Great Plains were based upon climate and topographic variables but did not evaluate the role of land use and cover (Augustine et al., 2012). Whereas recent work by Olimb et al. (2022) conducted comparable analyses, using climate, topography, and landcover as predictors of BTPD habitat in three Native nations of Montana. Our new models for the entire BTPD range identified similar effects of topography and climate, and additionally incorporated effects of land use. Our results reflect BTPD preference for deep, clayey-loam soils (with low percentage of sand) that facilitates burrowing and mound building, and their strong habitat association with grasslands in broad, flat plains where visibility is maximized (Augustine et al., 2012; Hoogland, 1995). The positive relationship we found with winter-spring precipitation reflects forage resources available during the key period of offspring production in the spring. Summer-fall precipitation also is important for BTPDs, particularly for enabling overwinter survival, but a large amount can cause tall vegetation that can impede colony growth (Bruggeman and Licht, 2020; Grassel et al., 2016), and also can potentially increase the presence of plague (Biggins et al., 2021).

Our model was trained on McDonald et al.'s (2015) dataset, which was (and to date still is) the only population survey available across the BTPD range. The dataset was ideal for creating a range-wide habitat suitability model because it was a systematic survey and it provided both presence and absence data. However, the data do have potential biases that are important to keep in mind when interpreting our model. McDonald et al. (2015) included a correction factor to account for the possibility that observers would miss small colonies (false negatives), but they did not account for potential sources of error that could lead to their values being overestimates of colony area (false positives). McDonald et al. (2015) found a 15 to 30 % false positive rate for a subsample of their dataset (state of Wyoming), and a follow-up study that used the same methodology found a 26 % overall false positive rate (state of Colorado in 2016) (Howlin and Mitchell, 2016). Although state biologists helped us remove false positives from our dataset, there were still likely false positives that remained, meaning that our model may harbor some over-estimates of suitable habitat. Moreover, our model does not consider prairie dog population densities, only estimated area of occurrences. Population densities of prairie dogs are rarely gathered when conducting large-scale population surveys, because of the considerable logistical effort entailed. Nevertheless, such data are valuable for informing management, as relatively high population densities reflect good habitat quality and are important for sustaining populations of associated species, especially predators like black-footed ferrets (Ceballos et al., 2010; Livieri et al., 2022). Finally, plague has dramatically influenced prairie dog population dynamics across much of their geographic range (Cully et al., 2010; Augustine et al., 2008a; Davidson et al., 2022), and the data we used to train our model is based on colony occurrences across landscapes where plague is now endemic. This should be kept in mind when interpreting our HSMs, although it is unlikely that the presence of plague has altered what our model identifies as suitable habitat. In any given year and location, some colony complexes are at a low point induced by a recent plague epizootic, while others are undergoing expansion/recovery following plague, and still others are at a high point in colony area. Our modeling approach averages across all of this variation in colony extent by using a survey of colonies across the entire range of the species, enabling the model to identify overall patterns of soils, climate, topography, and vegetation that are associated with BTPD colonies.

The development of our HSM was a collaborative process with local experts and land managers. The reviews we received from experts, managers, and the WAFWA PDCT were integral to improving the accuracy and applicability of our model. Through the process we were able to learn about and correct erroneous data points, model deficiencies, as well as how our model could be made most useful to managers. Increasingly, scientists and managers are working together to co-create such decision support tools (Schwartz et al., 2018; Sofaer et al., 2019). Insights from the experts and managers we collaborated with greatly improved the quality of our model and its on-the-ground utility for wildlife management.

Our aim was to produce a model that could identify for management agencies and NGOs the most biophysically suitable areas to focus on for BTPD ecosystem conservation. With conservation dollars limited, our maps (at 30 $m^2$ resolution) provide insights for strategic conservation planning, with a lens into the effects of climate change. They enable entities engaging in conservation actions such as restoration, conservation, management, and land protection to evaluate the distribution of suitable habitat on a given property, as well as within the broader surrounding landscape. Central to any conservation strategy is understanding the connectivity of suitable habitat, landownership, and how different areas fit into the broader landscape (Augustine et al., 2021; Rudnick et al., 2012). Our maps show how northeast New Mexico, southeast Colorado, northeast Wyoming, and western South Dakota harbor some of the largest remaining high-suitability grassland habitat for the BTPD ecosystem today, and that many of these areas remain strongholds into the future. Plague is common throughout these areas, so plague mitigation is likely to be an important management consideration where conservation efforts are focused. From a range-wide perspective, these regions may be some of the best to focus on for purchasing land and conservation easements to support the BTPD ecosystem and BFF recovery. In southeast Colorado, for example, there have been major efforts by NGOs to focus on private lands conservation, primarily through conservation easements and land acquisition for conservancies (Colorado Natural Heritage Program and the Geospatial Centroid, 2022). In addition, Colorado State Land Board has consolidated their holdings to create several large, contiguous properties that contain extensive BTPD habitat in southeast Colorado (Colorado Natural Heritage Program and the Geospatial Centroid, 2022).

Understanding the ecologically most suitable habitats for wildlife conservation is at the core of any conservation decision making, which our maps illuminate for the BTPD ecosystem. A critical next step in conservation planning for the BTPD ecosystem is to identify priority areas that not only consider this ecological landscape, but also the political, social, and threat landscapes (Ban et al., 2013; Miller et al., 2007; Niemiec et al., 2021; Pressey et al., 2007). This is especially important for contentious species like BTPDs where much of the suitable habitat occurs on private land, and for landscapes like the Central Grasslands that are highly fragmented with complex land ownership and jurisdictional boundaries (Augustine et al., 2021). As initiatives like the Central Grasslands Roadmap and America the Beautiful are implemented for North America's grasslands (Haaland et al., 2021), and others look to address the loss of temperate grasslands globally (Bardgett et al., 2021; Carbutt et al., 2017; Henwood, 2010), it will be key to identify landscapes that are not only ecologically suitable for wildlife conservation, but also have the social and political support to facilitate success. Conservation planning efforts such as these are urgently needed to address the global challenge of temperate grassland decline.

## Credit authorship contribution statement

Ana Davidson: Conceptualization, methodology, writing – original draft, editing and review, visualization, supervision, project administration.

Michelle Fink: Formal analysis, writing – editing and reviewing.

Michael Menefee: Conceptualization, visualization, writing – reviewing.

Lindsey Sterling-Krank: Conceptualization, visualization, project administration, funding acquisition, writing – review.

Bill Van Pelt: Funding acquisition, visualization, writing – editing and reviewing.

David Augustine: Conceptualization, methodology, writing – editing and reviewing, visualization.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

BTPD habitat suitability maps can be downloaded here: https://cnhp.colostate.edu/projects/hotr/#Downloads1.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110241.

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