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RESEARCH ARTICLE

Predicted future range expansion of a small carnivore: swift fox in North America

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Abstract

Context Small carnivores are declining globally due to a complex suite of threats. Conservation of these species requires an understanding of their distributions and potential responses to future land-use and climate change.

Objectives We modelled species-environment relationships of swift fox (*Vulpes velox*), a species of concern across their range. We developed spatial projections of current and future distribution to aid in conservation planning.

Methods We assembled swift fox occurrence data from managers and community science sources to develop ensemble distribution models. In addition to landscape and climatic predictors, we developed a model of red fox distribution to represent effects of competition. We forecasted spatial predictions into the year 2070 under two climate change scenarios representing high (SSP 5–8.5) and low (SSP 1–2.6) emissions scenarios.

Results Percent cover by grassland, mean annual precipitation, and minimum temperature of the coldest quarter were the three most important variables for swift fox distribution. Current suitable habitat for swift fox extends across 16 North American states and provinces. Future projections of swift fox distribution suggest an overall increase in area of swift fox suitable habitat under both emissions scenarios of > 56.9%, though patterns of gain and loss vary spatially.

Conclusions The expansion of suitable habitat in future scenarios reflects swift fox adaptability to multiple land uses in a period following multi-organizational conservation efforts. Our spatial projections can be used in conservation planning and can serve as a case study of a small carnivore species likely to recover under future change scenarios provided that threats are addressed and landscape-scale conservation efforts continue.

Keywords Swift fox · *Vulpes velox* · Species distribution model · Future change

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Introduction

Calls for conservation of small carnivore species are increasing across the globe (Belant et al. 2009; Do

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Linh San et al. 2013; Marneweck et al. 2021). While some small carnivore populations are increasing and are capable of living alongside human pressures (Bateman and Fleming 2012), 50% of small- and medium-sized carnivore species are currently threatened (Marneweck et al. 2021). Threats to small carnivores are diverse, including but not limited to: biological resource use, land use change, invasive species and disease, and energy production (Willcox 2020; Marneweck et al. 2021). Many of these threats are expected to increase under future change scenarios, and since small carnivores must cope with numerous and likely compounded stressors, some have argued that small carnivores are ideal sentinel species of global change (Marneweck et al. 2022; Jachowski et al. 2024). In addition to challenges of increasing threat pressure, many small carnivore species are considered 'data deficient' with unknown population trends, resulting in uncertainty for conservation practitioners (Marneweck et al. 2021). Considering this and their importance in ecosystems (Do Linh San et al. 2013; Marneweck et al. 2022), there is a need to understand both the current and future potential distribution for small carnivores under global change scenarios.

Species distribution models (SDMs) can help fill knowledge gaps and assist with conservation planning for threatened species at a broad spatial scale (Franklin 2013). SDMs relate environmental variables to species locations to predict distribution across landscapes, and these distributions can be extrapolated in space and time (Elith and Leathwick 2009). Importantly for small carnivores, which can be difficult to detect and research, SDMs can leverage presence data collected from diverse data sources (e.g., field surveys, community science sources) to make landscape-scale inference. When species-environment relationships are projected across time scales, SDMs can help managers and conservation practitioners anticipate effects of future change on species of interest. The resulting output from future projections can reveal range shifts, expansions, or levels of extinction risk (Thomas et al. 2004). Additionally, future distribution maps can help identify areas important for species conservation, such as locations with potential to serve as new habitat or climate refugia (Franklin 2013; Stralberg et al. 2018) or suitability for restoration efforts such as trophic rewilding or other reintroductions (Martínez-Meyer et al. 2006; Jarvie and Svenning 2018; Maes et al. 2019; Bellis et al. 2021).

Swift fox (*Vulpes velox*) is a small carnivore species of concern across much of its range, which has been subject to extensive restoration efforts for over 30 years (Kahn et al. 1997; Carbyn 1998; Dowd Stukel 2011). Swift fox were once widely distributed across the short- and mixed-grass prairies of the Great Plains but experienced precipitous declines typically attributed to predator eradication campaigns and land conversion in the late 1800s (Sovada et al. 2009). Swift fox populations have rebounded in some portions of their range due to both natural recolonization (Sovada et al. 2009) and reintroduction efforts (Carbyn 1998; Ausband & Foresman 2007a, b; Sovada et al. 2009; Sasmal et al. 2015). However, the latest assessment of swift fox distribution indicated that swift foxes were extant in only 44% of their historic range in the US and 3% in Canada (Sovada et al. 2009), and large gaps between occupied portions remain (Butler et al. 2020a). Within these unoccupied portions of historic range, restoration potential appears high given that the major threat of indiscriminate poisoning has been addressed by managers and that local suitability models suggest the availability of high-quality habitat for swift foxes (Alexander et al. 2016; Paraskevopoulou et al. 2021).Recently, reported sightings suggest that swift foxes are starting to cross those range gaps (MTFWP 2019) and are colonizing previously unoccupied habitats (Bjornlie 2018). Thus, there is a need to better understand factors influencing the current distribution of swift fox.

Similar to other threatened small carnivores, threats to swift fox are multifaceted and likely to change over time. Several studies suggest that swift fox rely on large tracts of short- or mixed-grass prairie and thus can be sensitive to fragmentation via other landcover types or human infrastructure (e.g., roads, gas wells; Kamler et al. 2003; Russell 2006; Butler et al. 2020a, b). Additionally, some have posited that pesticide and rodenticide use are one factor preventing swift foxes from using crop fields in the northern part of their range (Carbyn et al. 1994). However, populations persist in agricultural mosaics elsewhere (Sovada et al. 1998; Werdel et al. 2022) and in habitat types other than grassland (e.g., sagebrush steppe; Olson and Lindzey 2002). In addition, given their central trophic position in the predator community, swift foxes can be negatively impacted by interspecific competition. Specifically, non-native red fox (*Vulpes vulpes*) arrived in areas overlapping swift fox range between 1930–1970 (Kamler and Ballard 2002) and have been proposed as a limiting factor to swift fox range recolonization (Moehrenschlager et al. 2004). To date, there have not been attempts to model swift fox distribution as a product of these potential limiting factors.

In addition to current threats, impacts of future change on swift fox are of interest for conservation planning. Land use change, increased fragmentation, and altered patterns in human development are predicted across swift fox range in the Great Plains (Shafer et al. 2014; Ojima et al. 2021) and are likely to affect future habitat suitability given their typical reliance on large tracts of native grassland (Butler et al. 2020b). Additionally, though swift foxes occur across a wide climate gradient, future swift fox populations may respond to climate change directly at the distribution level (i.e., altered patterns in precipitation or temperature). Precipitation effects on population dynamics have been observed in swift fox (e.g., declines following multi-year droughts; Herrero et al. 1991) and other small canid species (Cypher et al. 2000, 2017; Bakker et al. 2021). Winter severity is another climatic variable that could influence swift fox distribution, as winter conditions have been suggested to alter competitor dynamics (Herrero 2003) and have influenced genetic connectivity models (Schwalm 2012). Future swift fox distribution will likely be influenced by multiple aspects of future change, thus underscoring the need and utility of species distribution projections that can incorporate both climatic and land cover predictors.

Based on past studies, we compiled a suite of landscape and climatic predictors to explain swift fox current distribution (Table 1). We predicted that land cover would have the greatest explanatory power for swift fox current distribution, and thus future scenarios involving reductions in grassland composition and altered configuration (i.e., smaller or

Table 1 Justifications for inclusion of land cover, edaphic, topographic, climatic, and biotic predictors of swift fox distribution

Predictor		Effect	Justification
Land cover	Urban	↓↑	Predicted avoidance of urban land cover in favor of native grassland. However, some evidence of positive associations with roads (Hines and Case 1991; Nevison 2017) and other development (e.g., gas wells) may not be avoided (Butler et al. 2020b)
	Cropland	↓	Selection of native grassland over cropland cover (Kamler et al. 2003; Sasmal et al. 2011), though swift fox use dryland crop fields in Kansas (Sovada et al. 2001)
	Grassland	↑	Well-documented requirements for large tracts or proportions of native grassland (Kamler et al. 2003; Butler et al. 2020b; Werdel et al. 2022)
	Diversity of land cover	↓	Space-use requirements for large tracts or proportions of native grassland (Kamler et al. 2003; Butler et al. 2020b) suggest a negative effect of land cover diversity. Werdel et al. (2022) found that occupancy was highest at intermediate land cover diversity
Edaphic	Soil % clay content	↓↑	Loamy textures are suitable for dens. Predicted effect is quadratic to represent intermediate quantities of sand, clay, and silt in loamy-textured soil (Pruss 1999; Jackson and Choate 2000; Harrison 2003; Werdel et al. 2022)
Topographic	Terrain roughness	↓	Flat terrain (Pruss 1999; Russell 2006); weak negative effect of roughness (Butler et al. 2020a, b)
Climatic	Mean annual precipitation	↑	Density declines after multi-year drought (Herrero et al. 1991); small canids negatively respond to drought (Cypher et al. 2000; Bakker et al. 2021); Mean annual precipitation was an influential variable in genetic connectivity models (Schwalm 2012)
	Winter severity	↓	Herrero (2003) listed winter severity as a factor influencing swift fox numbers
Biotic	Red fox distribution	↓	Considered to limit swift fox expansion (Moehrenschlager et al. 2004). Red fox are known to outcompete other smaller fox species, such as Arctic foxes (Hersteinsson and Macdonald 1992; Rodnikova et al. 2011; Gallant et al. 2013)

The direction of predicted effects is indicated via up or down arrows more fragmented grassland patches) would result in reduced suitability and total area of swift fox range. We predicted a positive relationship between swift fox distribution and annual precipitation, and a negative relationship with winter severity. Because swift fox use dens year round (Kilgore 1969; Egoscue 1979) and typically prefer flat terrain (Pruss 1999; Russell 2006), we predicted that swift fox distribution would be limited to areas with loamy soils and areas with low values of terrain ruggedness. We expected that swift fox distribution would be negatively related to red fox distribution due to interference competition. By providing the first range-wide species distribution model for swift fox and by predicting how the species will be distributed under future global change scenarios, our findings provide important guidance for management of this species of conservation need. More broadly, our approach highlights the utility of SDMs to guide current and future efforts to restore threatened small carnivores.

Materials and methods

Study extent and occurrence data

To define a study area extent we applied a 100 km buffer to historic swift fox range (Moehrenschlager and Sovada 2016; Fig. 1). We downloaded occurrence data for both red fox and swift fox from two publicly available databases: the Global Biodiversity Information Facility (GBIF; gbif.org; Accessed 13 July 2023) and iNaturalist.org (Accessed 13 July 2023) from 2006 to present within the study extent (Supplemental Figs. S2, S4). GBIF includes occurrence records from museum collections, university records, and research-grade community science contributions, while iNaturalist.org is a website containing only observations submitted by community scientists. Research-grade community science records in both GBIF and iNaturalist are submitted with a photo, date, and geographic coordinates. Further, the taxonomy of these records is verified through consensus by the online naturalist community. Therefore, we only retained community science observations classified as research-grade. We removed data with missing or duplicate geographic coordinates or with a coordinate uncertainty of greater than 5000 m. We also received 4583 additional swift fox locations directly from 10 state and provincial wildlife management agencies and natural heritage programs. These data were derived from incidental observations by agency staff and partners, camera trapping, and live trapping efforts from 2006 through 2022 (Supplemental Table S1).

Because the occurrence data are presence-only and result from opportunistic detections rather than systematic surveys, sampling bias may affect SDM performance and prediction (Beck et al. 2014). Clustered detections resulting from unstructured data collection can lead to overrepresentation of environmental conditions where sampling effort was high in SDMs (Kadmon et al. 2004; Anderson and Gonzalez 2011). By filtering areas with dense occurrence records, spatial thinning can mediate bias resulting from spatially autocorrelated occurrence data while allowing for straightforward evaluations of model performance (Aiello-Lammens et al. 2015). We spatially thinned all occurrence records to retain a minimum nearest neighbor distance of 12 km, which is the average dispersal distance reported for swift fox (Schauster et al. 2002; Ausband & Foresman 2007a, b).

Environmental data

We developed current and future land cover predictors using global land-use and land-cover change data projected by Chen et al. (2022). These data include the distribution of 20 plant functional types at 1 km resolution from 2015–2100 according to the Intergovernmental Panel on Climate Change (IPCC) socioeconomic and climate change scenarios (SSP). The SSPs relate socioeconomic growth patterns to the previously used representative concentration pathways approach and were adopted in Phase 6 of the Coupled Model Intercomparison Project (CMIP6), an international framework which coordinates experiments to model and project climate change (van Vuuren et al. 2014). We selected two SSPs to represent the extremes of predicted outcomes for future predictions in the year 2070: an extreme low end with declining emissions after 2020 (SSP 1–2.6) and an extreme high end with increasing greenhouse gas emissions (SSP 5–8.5; IPCC 2021).

We generated land cover predictors using the Chen et al. (2022) dataset by calculating percent cover by plant functional types within 35 km^2 cells (Table S8). To represent current conditions, we used rasters developed from land cover data collected in

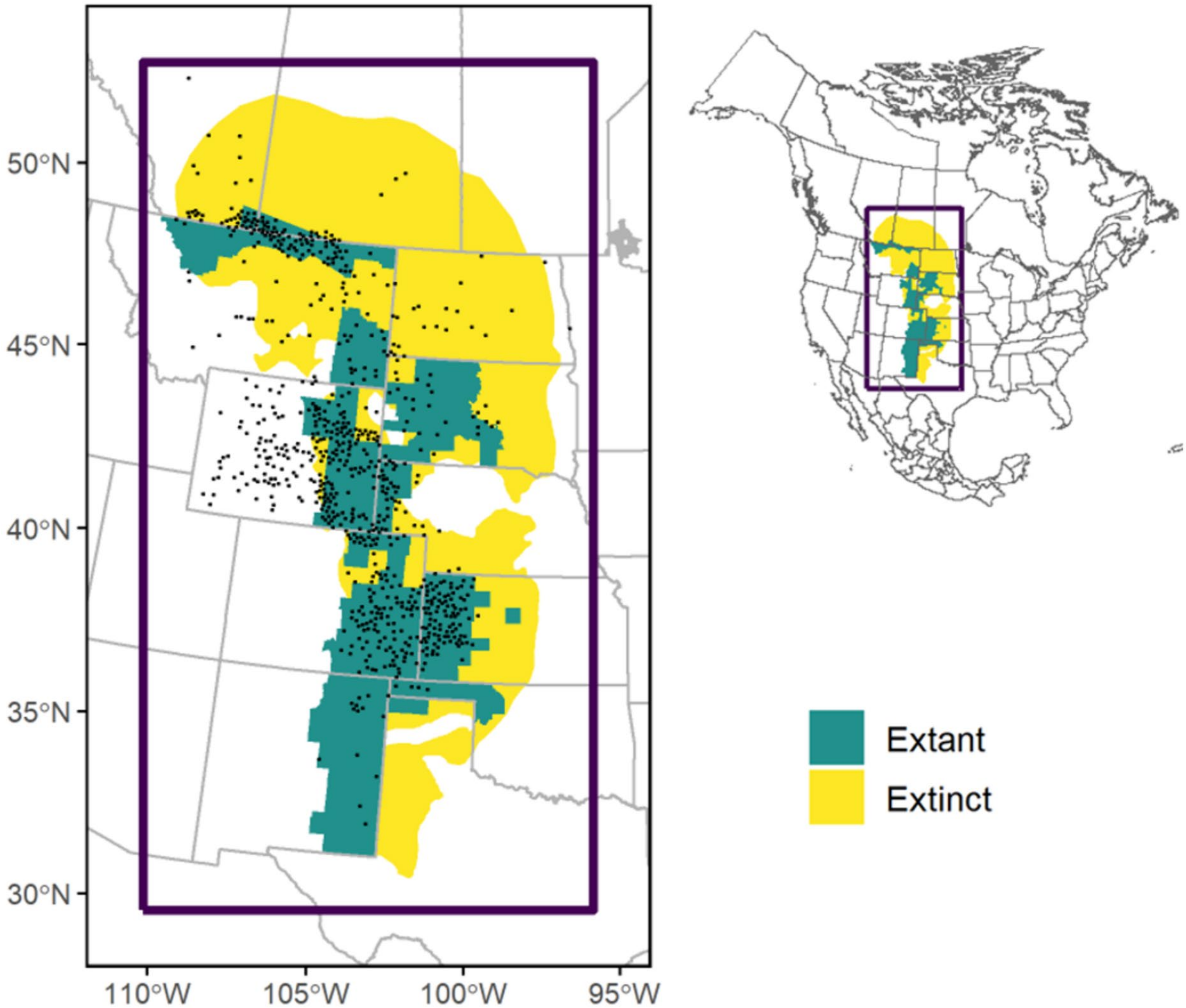


Fig. 1 Study area extent relative to current and historic geographic range of swift foxes (modified from Moehrenschlager and Sovada 2016). Black points depict spatially thinned records used to develop distribution models. Moehrenschlager and Sovada (2016) *Vulpes velox*. The IUCN Red List of Threatened Species

2015, which is the earliest year represented in this dataset (Chen et al. 2022). We selected a resolution of 35 km^2 because this represents an area accessible to swift fox (approximately 10 km^2 larger than average reported home range size for swift fox; see table in Butler et al. 2020b). We developed a percent cover by grassland (GRASS) raster by pooling plant functional types corresponding to cool season grass and mixed C3/C4 grass into a single grassland cover type prior to summation within each 35 km^2 cell. We calculated the Shannon Diversity Index (SHDI) of land cover types within each 35 km^2 cell as a measure of landscape configuration (i.e., fragmentation). Class cover and local landscape diversity metrics were calculated using the 'landscapemetrics' package in R v4.1.3 (R Core Team 2021, Hesselbarth et al. 2019). We repeated these procedures to develop the same land cover predictors for year 2070 under the two selected SSPs.

We downloaded climate rasters from the WorldClim bioclimatic variables dataset at 30 s resolution (Table S8; WorldClim 2022; Accessed on 28 July 2023). Bioclimatic variables for near current conditions were developed using annual averages between

1970–2000 (Fick and Hijmans 2017). We selected bioclimatic predictors BIO6 (minimum temperature of the coldest month), BIO11 (mean temperature of the coldest quarter; COLDTEMP), and BIO12 (annual precipitation, PRECIP) to represent hypothesized effects of winter severity and mean annual precipitation, and resampled each raster to 35 km^2. For future climate predictors, we downloaded rasters for 10 downscaled CMIP6 global circulation models (GCM) for which bioclimatic variables were available in the period 2061–2080 (ACCESS-CM2, CMCC-ESM2, EC-Earth3-Veg, GISS-E2-1-G, INM-CM5-0, IPSL-CM6A-LR, MIROC6, MPI-ESM1-2-HR, MRI-ESM2-0, UKESM1-0-LL) and averaged the GCMs to address uncertainties inherent to individual models (Thuiller et al. 2019).

To develop an edaphic predictor, we downloaded global percent clay content at 30 cm depth (CLAY; Hengl 2018). We also developed a topographic predictor, terrain ruggedness index (TRI; Riley et al. 1999) from an elevation layer with 30 arc second resolution derived from Shuttle Radar Topography Mission (Hijmans et al. 2005). We resampled both soil and topography rasters to 35 km^2 resolution (Table S8). We assumed these predictors were static, and thus used the same soil and topography rasters for current and future distribution models. We centered and scaled rasters that were not expressed as percentages (i.e., TRI, SHDI, climate variables) to a mean of 0 and standard deviation of 1 prior to analysis. All environmental predictor variables were transformed to Albers Equal Area projection (EPSG:5070) using nearest neighbor resampling. All model calibration, evaluation, and fitting procedures described for swift fox were repeated to develop an environmental predictor of red fox distribution (REDFOX; Appendix 1).

Model calibration, evaluation, and fitting

We used the study extent as the calibration area from which to draw 10,000 background points for both species (Appendix 1). We partitioned occurrence and background data for validation and evaluating model performance using longitudinal bands (Supplemental Fig. S1). In contrast to randomly splitting occurrence data into training and testing datasets, spatial bands test model transferability through comparison of one geographic band relative to a separate geographic band (Roberts et al. 2017; Santini et al. 2021). Between two and 20 bands were tested, and splitting the occurrence data into two bands was the optimal approach to minimize spatial autocorrelation, environmental similarity, and the differences in amount of data among partition groups (Velazco et al. 2019, 2022). Because collinear predictor variables can lead to overfitting and inaccurate interpretation of significance (Dormann et al. 2013; De Marco and Nóbrega 2018), we calculated Pearson's correlation coefficient and variance inflation factors among candidate rasters. We used thresholds for retention of 0.7 and 2.5, respectively. Climatic variables for temperature were collinear, so we retained BIO11 (mean temperature of coldest quarter) and removed BIO6 (minimum temperature of coldest month). Percent urban cover had a VIF score of 2.6 and was removed from further analysis of swift fox distribution.

We ran species distribution models using six different algorithms: random forest (RAF), support vector machine (SVM), neural networks (NET), generalized additive models (GAM), generalized linear models (GLM), and generalized boosted regression (GBM). We compared the performance of each model using the true skill statistic (TSS) and area under the receiver operating curve (AUC). Ensemble modeling can address uncertainty and biases among model algorithms (Hao et al. 2019), which is particularly useful for cryptic or sensitive species (Ramirez-Reyes et al. 2021), so we developed a TSS-weighted ensemble for current distribution from all algorithms with an AUC score of > 0.7. We created continuous maps of relative habitat suitability by spatially projecting environmental relationships predicted by ensemble models using the *sdm_predict* function in 'flexsdm.'

To compare range size relative to future scenarios, we binarized habitat suitability according to the threshold value at which sensitivity and specificity was maximized. Cells greater than this threshold were considered suitable and included in area calculations and those cells with values lower than the threshold were considered unsuitable and thus not included in area calculations. We used the 'landscapemetrics' package to calculate patch area of predicted binary suitable habitat for swift foxes, and then constrained the binary output to only include patches greater than 70 km^2 (i.e., two grid cells representing a 10 km buffered swift fox home range) to remove small, isolated cells of predicted habitat unlikely to support a population. We used the 'flexsdm' package for all pre-modelling, model fitting and validation, and post-modelling procedures.

To evaluate the contribution of each variable to estimates of distribution, we used model-independent variable importance procedures described by Thuiller et al. (2009) in which Pearson's correlation (r) is calculated between the predicted values of the original dataset and predictions in which one of the variables has been randomly permuted. We calculated variable importance from each algorithm used in the final ensemble. We examined partial dependence plots and predictive maps to infer the direction of effects on suitability for each variable.

Future projections

We projected the relationships into the future by applying the ensemble model to a set of rasters containing conditions for each environmental predictor in the year 2070. Similar to methods used for current map projections, we used the *sdm_predict* function in 'flexsdm' to generate both continuous suitability maps and binary predictions using the threshold at which sensitivity and specificity was maximized. We again constrained the predicted binary suitable habitat for swift fox to only include patches greater than 70 km^2 in area. From the rasters of predicted binary habitat suitability, we calculated the area of suitable habitat in square kilometers. We examined future changes in habitat suitability relative to current conditions by subtracting current, continuous raster values of relative habitat suitability from raster values predicted in the year 2070. We summarized the mean differences in all raster values per state or province. Additionally, we subtracted binarized predictions of current habitat suitability from binary values predicted in the year 2070, and categorized results as 'loss', 'gain', or 'stable' based on whether the future value minus the current value was equal to − 1, 1, or 0, respectively.

Results

We obtained 4743 records for swift fox. After removing duplicates and applying 12 km nearest neighbor geographic filtering, 739 were retained for modeling of swift fox (Supplemental Fig. S2). Swift fox distribution was modelled as a function of GRASS, SHDI, CLAY, TRI, PRECIP, COLDTEMP, and REDFOX (Appendix 1, Supplemental tables S5, S6). Six algorithms exceeded an AUC of 0.7 and were included in the ensemble of swift fox current distribution (Table 2). The mean weighted swift fox ensemble model had an AUC score of 0.824 (SD = 0.077) and a TSS of 0.503 (SD = 0.165). The suitability threshold at which the specificity and sensitivity was maximized (i.e., maximum TSS) was 0.067. Continuous values for swift fox suitability under current conditions ranged from 0.001–0.521 and an area of 1,025,472 km^2 was above the threshold which maximizes TSS for binary prediction of habitat (Supplemental Table S2). Across the six algorithms used in the ensemble, mean importance scores were highest for PRECIP, GRASS, and COLD TEMP (Table 3).

Maximum values of swift fox continuous habitat suitability were lower than under current conditions for both SSP1-2.6 and SSP5-8.5 (Maximum = 0.420 and 0.430, respectively). However, the total area over the threshold of binary habitat suitability for swift fox increased in both future scenarios (Fig. 2, Supplemental Table S2). Under SSP1-2.6, binary predictions of swift fox suitable habitat increased to 1,609,431 km^2 (56.9% increase) and under SSP5-8.5, suitable habitat increased to 1,664,065 km^2 (62.3% increase; Fig. 2). Areas of gain and loss varied spatially, with most increases in suitable habitat for swift fox occurring at the northeastern edge of swift fox range in the Dakotas and prairie provinces of Canada (Fig. 3). Less than 12% of current swift fox distribution is predicted to be lost under future scenarios (8.3% under SSP 5–8.5; 11.1% under SSP 1–2.6), largely

Table 2 Performance metrics for swift fox distribution models

Algorithm	TSS (SD)	AUC (SD)	Threshold value
NET	0.573 (0.114)	0.836 (0.048)	0.0861
GAM	0.527 (0.104)	0.811 (0.059)	0.0791
GBM	0.447 (0.111)	0.783 (0.058)	0.0728
RAF	0.456 (0.148)	0.782 (0.087)	0.604
GLM	0.42 (0.181)	0.763 (0.108)	0.0799
SVM	0.444 (0.113)	0.76 (0.038)	0.0813

Ensemble models were developed for each species from a true skill statistic (TSS) weighted mean of all algorithms with an area under the curve (AUC) score > 0.7

NET Algorithms included neural networks, *GLM* generalized linear, *GAM* additive models, *RAF* random forest, *GBM* generalized boosted regression models, *SVM* support vector machine

Table 3 Variable importance scores from all algorithms used to develop ensemble models of swift fox distribution

Variable	Algorithm						Weighted mean
	RAF	GLM	GAM	NET	SVM	GBM	
PRECIP	**0.275**	**0.264**	**0.192**	**0.490**	0.295	**0.261**	0.303
GRASS	0.096	**0.334**	0.043	**0.441**	**0.469**	**0.163**	0.258
COLD TEMP	**0.250**	0.008	0.315	**0.337**	0.384	0.096	0.232
TRI	**0.121**	**0.058**	**0.385**	0.145	**0.518**	0.090	0.210
RED FOX	0.052	0.003	**0.333**	0.000	**0.780**	0.028	0.180
CLAY^2	0.084	0.054	0.072	0.029	0.373	**0.108**	0.112
SHDI^2	0.030	0.009	0.001	0.006	0.327	0.024	0.059

Importance scores were calculated using methods described by Thuiller et al. (2009) such that Pearson's correlation (r) is calculated between the predicted values of the original dataset and predictions in which one of the variables has been randomly permuted

Higher values indicate more influence of the variable on that model

The three most important variables for each algorithm are highlighted in bold, and abbreviations of algorithm names are introduced in Table 2

As in the development of the ensemble distribution model, mean values are weighted by each model's true skill statistic (TSS)

Variables include mean annual precipitation (PRECIP), percent cover by grassland (GRASS), minimum temperature of the coldest quarter (COLD TEMP), terrain ruggedness index (TRI), red fox distribution (RED FOX), percent content of clay in the soil (CLAY), and Shannon's diversity index of land cover types (SHDI) within 35km^2 raster cells

in currently unoccupied portions of the southwestern United States and along the western edge of the distribution (Fig. 2, Table S2). Spatial patterns of expansion and minimal loss in swift fox distribution correspond with projected changes in modelled climatic variables and percent cover by grassland (Fig. 4).

Discussion

Through collaboration with management agencies and natural heritage programs, we assembled a dataset of swift fox occurrences to model their current distribution and conduct the first projection of swift fox responses to future change scenarios. The resulting dataset consists of > 4700 swift fox locations collected since the latest mapping of their range in 2006 (Sovada et al. 2009), and includes observations in a variety of land cover types (e.g., grassland, cropland, shrubland) across nine states and two provinces. Percent cover by grassland and two climatic variables were the three most important predictor variables for our ensemble model of swift fox distribution, but spatial projections of suitable habitat span multiple land cover types. Because of these relationships with land cover and projected trends in climate, models predict a large expansion of swift fox suitable habitat by the year 2070 under both a low-emissions scenario (SSP 1–2.6) and an extreme high emissions scenario (SSP 5–8.5) to over 1,600,000 km^2. Expansion of swift fox suitable habitat is most pronounced on the northeastern edge of swift fox range, similar to northward range shifts also projected in the region for other vertebrate species (e.g., avian regime shifts, Roberts et al. 2019; black-tailed prairie dog suitable habitat, Davidson et al. 2023). However, unlike these other studies in the Great Plains, we did not see concomitant declines in the southern or central portion of swift fox range.

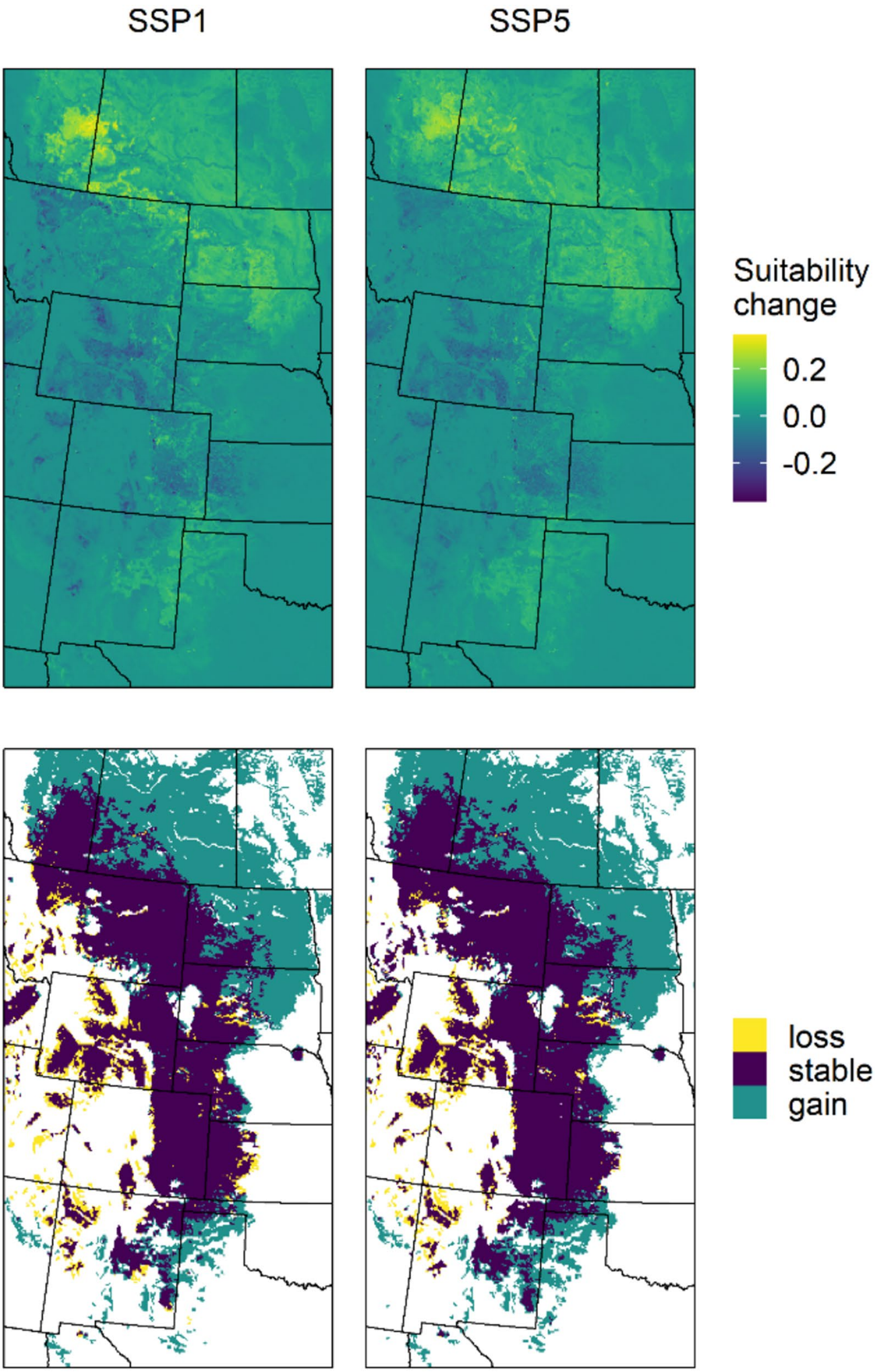
Our measure of winter severity, minimum temperature of the coldest quarter, was an important variable for ensemble models of swift fox distribution. Current suitable habitat for swift foxes appears to be highest at intermediate values, suggesting they could be limited in the north by winter severity. Decreased winter severity (i.e., warmer winter temperatures) in the northeastern portion of our study extent appears to be one driver of projected future increases in swift fox suitable habitat. Winter severity has been suggested as a factor influencing swift fox numbers in Canada (Herrero 2003), and has been shown to limit red fox density in Europe and Asia (Bartoń and Zalewski 2007). Severe winters may limit swift fox distribution via decreased prey abundance and the resulting stress on fox energetics. Prey availability already tends to be lower in the winter, especially in the northern part of swift fox range where many prey resources migrate, hibernate, or become dormant (Klausz 1997). Swift fox rely on small mammals in winter (Hines and Case 1991), whose activity and abundance levels can be negatively impacted by extreme winter conditions (Klausz 1997). Potentially in response to this reduced prey availability, swift foxes travel longer distances and at faster rates during the winter relative to the summer (Covell et al. 1996). Though increased winter movements and rates have not corresponded to higher energy expenditure (Covell et al. 1996), winter nutritional deficiencies and mortalities attributed to starvation have been observed at the northern extent of current swift fox range (Klausz 1997).

Our models predicted a negative relationship between swift fox habitat suitability and mean annual precipitation, the second climatic variable we modelled. Localized areas of suitable habitat loss along the periphery of swift fox distribution are expected to see an increase in mean annual precipitation, while the drier conditions predicted in portions of the northern Great Plains contribute to the northeastern expansion of swift fox distribution. The negative relationship contrasts our predictions made based on the positive relationship between precipitation and other fox population dynamics (Cypher et al. 2000; Bakker et al. 2021). However, these studies have been able to capture interannual variability versus annual means. When considering distribution, lower mean annual precipitation may be correlated with the vegetation structure preferred by swift fox (i.e., short-stature grasses; Harrison & Schmitt 2003; Sasmal et al. 2011).

In addition to the direct responses to climate variables, swift fox distribution was influenced by land cover. Percent cover by grassland was unsurprisingly an important variable in our models of swift fox current and future distribution. Across their range, contiguous tracts of grassland are frequently strong predictors of swift fox resource use and occupancy (Kamler et al. 2003; Butler et al. 2020b; Werdel et al. 2022), and survival (Butler et al. 2020a). Overall cover by grasslands is predicted to increase in our study area by 4.1–6.8% in 2070, according to projections developed by Chen et al. (2022). While the overall percent increases in grassland cover are modest, cover by grassland becomes more contiguous under both future scenarios in the Dakotas and southern Canada, areas where our models predicted substantial increases in swift fox suitable habitat (Fig. 4). Positive effects of future change on habitat have also been predicted for San Joaquin kit fox, whose modelled population sizes increased by 7% in response to vegetation structure changes under climate scenarios (Nogeire-McRae et al. 2019).

Not all predicted suitable habitat for swift fox is in areas dominated by grassland cover. Under current conditions, 23% of predicted suitable habitat was in areas predicted to be covered by crop fields, and this increased under both future scenarios (35% and 38% for SSP1-2.6 and 5–8.5, respectively).Potential habitat in non-grassland cover types is expected, given swift fox persistence in areas with crop cover in some parts of their range (Sovada et al. 2001; Werdel et al. 2022). Swift fox occupancy in Kansas was insensitive to the amount of row crop agriculture present, and authors suggested instead that non-native vegetation planted as part of the Conservation Reserve Program (USDA Farm Service Agency 2018) currently limit distribution on the eastern edge of swift fox range (Werdel et al. 2022). Many presence records used to build distribution models were from such areas where fox regularly use dryland agriculture fields and from sagebrush steppe, and all records are from a period in which swift fox populations have rebounded from historic lows due to both natural recolonization and restoration efforts. Swift fox presence and current suitability predictions in "less typical" habitats provide evidence of the species' adaptability. However, it is not well-known whether crop fields or sagebrush-dominated areas serve as high-quality swift fox habitat in terms of population demography. Other small carnivores that are considered habitat specialists can succeed in agricultural settings (e.g., servals in South Africa are thought to be wetland specialists but had similar density estimates in wetlands and farmlands; Ramesh & Downs 2013). While occurrence records and models show that swift fox use certain atypical habitats, more research is warranted to elucidate whether survival rates indicate that these habitats are serving as sinks or ecological traps.

Spatial predictions of red fox distribution were developed to model interspecific competition, but red fox distribution was not a top predictor for swift fox models. Suitable habitat for red fox was largely limited to areas surrounding urban centers and high elevation mountain ranges, with other patches distributed throughout the Great Plains (Supplemental


SSP1
SSP5
Suitability change
0.2
0.0
-0.2
loss
stable
gain

◂**Fig. 2** Differences between spatial predictions of current swift fox habitat suitability and habitat suitability predicted under scenarios SSP1-2.6 and SSP5-8.5 in the year 2070. Current relative habitat suitability values resulting from spatial projections of ensemble distribution models were subtracted from raster values estimated by ensemble models for the year 2070 (top). Habitat suitability was also binarized according to the threshold at which sensitivity and specificity was maximized (i.e., cells greater than this threshold were considered suitable, cells with values lower than the threshold were unsuitable). Changes in these binary indices of habitat suitability (bottom) were again calculated by subtracting current raster values from those projected in 2070, and then classified 'loss', 'gain', or 'stable'

Fig. S3). Red fox are highly adaptable, and their habitat selection in the Great Plains specifically can vary by landscape configuration. For example, studies in North Dakota revealed that red fox selection of planted crop cover and movements within it varied with the amount of grassland on the landscape (Phillips et al. 2003, 2004). Patchiness of predicted red fox suitable habitat helps explain why it was not a top predictor for swift fox suitable habitat. If red fox suitable habitat exclusively contained urban areas or high topographic ruggedness, one might expect a stronger negative effect for swift fox models. Additionally, both species had predicted suitable habitat in cropland. In contrast to swift fox, future suitable habitat for red fox did not dramatically increase; projections in 2070 include a slight decrease under SSP1-2.6 and a slight increase under SSP5-8.5. These minimal changes in future distribution likely reflect the importance of percent urban cover on red fox models. Though urban cover is projected to increase in our study system under both future scenarios in our study area (Supplemental Table S3, Chen et al. 2022), urban area remains small and concentrated (< 40,000 km^2).

Our models capitalized on future land cover layers at 1 km resolution, allowing us to incorporate land cover and anthropogenic effects into projections. We acknowledge that this data layer was static (i.e., developed in 2015, the median of our occurrence data date range), and this may impact our projections since land cover can change. From this dataset, we used percent urban land cover as an index of human development, and it was an important contributor to red fox distribution models. However, other forms of anthropogenic infrastructure were not represented and would be useful for species in rural settings. For example, development of new roads, oil and gas wells, or solar farms could affect the suitability of fox habitat (e.g., Hines & Case 1991; Nevison 2017). To our knowledge, spatial predictors of these disturbances are not yet available into the future and at a continental or global scale. While our models did not incorporate energy or other forms of rural development, spatial layers resulting from our SDMs could be used to inform siting and policy decisions (e.g., future renewable energy siting; Ashraf et al. 2024). Additionally, climatic variables were important for predictions of both species' distributions, however mean and minimum values do not necessarily capture the climate variability that is typical of the Great Plains and is predicted to increase in the future (Hicke et al. 2022). Incorporation of extreme weather events would better characterize climate dynamics in the Great Plains and projections of wildlife population responses. Our models had high predictive performance (AUC

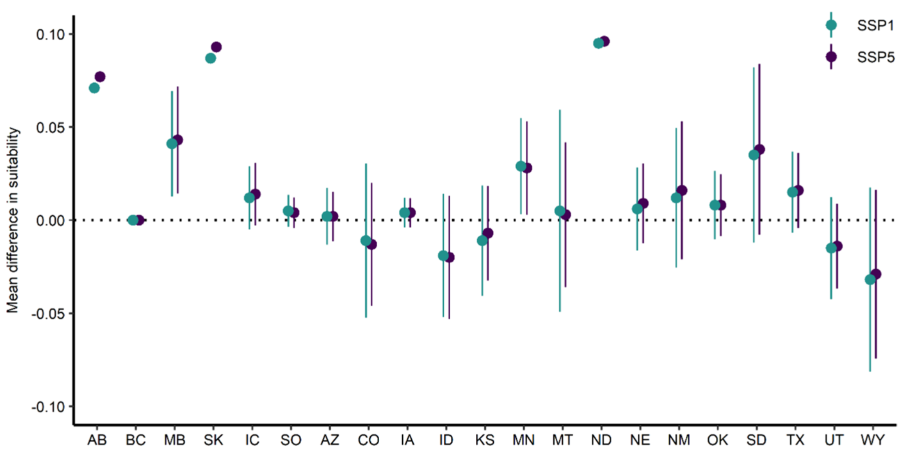


Fig. 3 Mean differences (and standard deviation) in habitat suitability values resulting from ensemble species distribution models for swift foxes in each state or province between current and future scenarios (SSP1, SSP5) in the year 2070

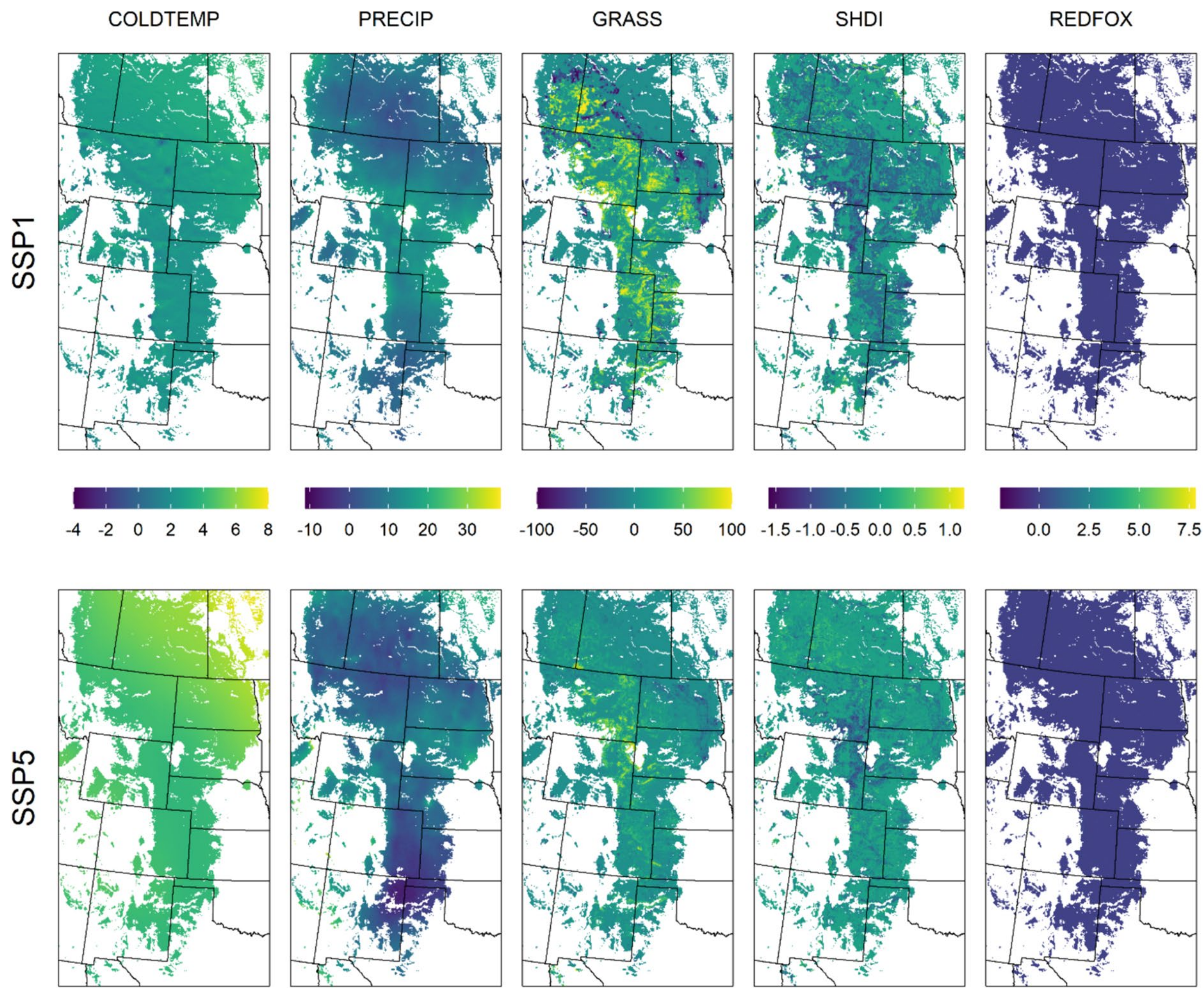


Fig. 4 Differences in spatial predictions between future conditions and current conditions for each predictor of swift fox distribution under two scenarios, SSP 1–2.6 (top) and SSP 5–8.5 (bottom). Maps were developed by subtracting current raster values from future raster values and cropping the output to the extent of suitable habitat predicted for that scenario. Climate predictors include the minimum temperature in the coldest quarter (COLDTEMP) and mean annual precipitation (PRECIP). Land cover predictors include percent cover by grass (GRASS) and Shannon's diversity index of land cover (SHDI) within 35 km2 cells. Red fox distribution was also modelled and included as a predictor (REDFOX, Appendix 1)

values > 0.8), but development of more dynamic and precise future predictors could further refine the projections of species distributions in the Great Plains.

Ultimately, our projections of swift fox distribution highlight the restoration potential of the Great Plains. A majority of current suitable habitat for swift fox is predicted to be stable in the year 2070. Swift fox across their range seem well-positioned for recovery pending that species-climate relationships remain constant (Pearson and Dawson 2003) and that swift fox populations are able to remain at sufficient densities. Restoration potential is particularly high in the northern Great Plains, where areas of future swift fox habitat expansion overlap predictions of suitable habitat for a keystone species in the system, black-tailed prairie dogs (Kotliar et al. 2006; Davidson et al. 2023) and where active restoration efforts are currently underway (Paraskevopoulou et al. 2021). Recent research has shown that social tolerance for swift foxes in this region is high relative to other species in need of restoration (Titus et al. 2024), which further contributes to the area's potential for swift fox recovery.

Our work is an example of how species distribution models can be collaboratively produced to inform small carnivore conservation and future planning. Through cooperation with state and provincial agencies, we generated a rangewide presence dataset integrating managers' survey results and community science records, and from these developed spatial predictions of current and future distribution. We found that a small carnivore of conservation concern has the potential to respond positively to future change. Importantly, these patterns are likely an artifact of decades of swift fox and grassland conservation efforts by tribes, agencies and organizations across their historical range that have been, in part, guided by the Swift Fox Conservation Team (Dowd Stukel 2011). Thus, in the face of global declining trends, we highlight a case study in which a small carnivore species is likely to recover under future change scenarios provided that primary threats are addressed and proactive restoration continues.

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Author contributions All authors contributed to the study conception and design. Data collection and analysis were performed by Dana Nelson. The first draft of the manuscript was prepared by Dana Nelson and David Jachowski. All authors contributed to subsequent drafts and gave final approval for publication.

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Data availability The data that support the findings of this study are available upon reasonable request from the corresponding author, but restrictions apply. Occurrence data are sensitive and were used under license from multiple organizations, and so are not publicly available. Data are located in controlled access data storage at Clemson University.

Declarations

Conflict of interest The authors declare no competing interests.

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