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RESEARCH ARTICLE

From past habitats to present threats: tracing North American weasel distributions through a century of climate and land use change

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Abstract
Context Shifts in climate and land use have dramatically reshaped ecosystems, impacting the distribution and status of wildlife populations. For many species, data gaps limit inference regarding population trends and links to environmental change. This deficiency hinders our ability to enact meaningful conservation measures to protect at risk species.
Objectives We investigated historical drivers of environmental niche change for three North American weasel species (American ermine, least weasel, and long-tailed weasel) to understand their response to environmental change.
Methods Using species occurrence records and corresponding environmental data, we developed species-specific environmental niche models for the contiguous United States (1938–2021). We generated annual hindcasted predictions of the species' environmental niche, assessing changes in distribution, area, and fragmentation in response to environmental change.
Results We identified a 54% decline in suitable habitat alongside high levels of fragmentation for least weasels and region-specific trends for American ermine and long-tailed weasels; declines in the West and increased suitability in the East. Climate and land use were important predictors of the environmental niche for all species. Changes in habitat amount and distribution reflected widespread land use changes over the past century while declines in southern and low-elevation areas are consistent with impacts from climatic change.
Conclusions Our models uncovered land use and climatic change as potential historic drivers of population change for North American weasels and provide a basis for management recommendations and targeted survey efforts. We identified potentially at-risk populations and a need for landscape-level planning to support weasel populations amid ongoing environmental changes.

Keywords Least weasel · Long-tailed weasel · American ermine · *Mustela* · *Neogale* · Environmental Niche Modelling (ENM)

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10980-024-01902-3.

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Introduction

Over the past century, rapid changes in climate and land use have profoundly altered Earth's ecosystems, impacting wildlife populations at unprecedented scales (Hoffmann et al. 2011; Ceballos et al. 2017; Brodie et al. 2021). A recent study of 177 mammals found 40% have experienced drastic population declines while most had lost over 40% of their geographic range (Ceballos et al. 2017). Habitat loss is often cited as the most influential driver of decline and agriculture alone ranks as the primary threat to 35% of at-risk mammals (Hoffmann et al. 2011; Brodie et al. 2021). However, changing climatic conditions are increasingly resulting in poleward and elevational shifts in environmental conditions leading to range shifts where species are able to track environmental conditions and range contractions where they cannot (Chen et al. 2011; Williams and Blois 2018; Brodie et al. 2021). Unfortunately, the interactive impacts of climate and land use change also often magnify impacts on species beyond that of any individual factor (Newbold 2018).

In the United States, post-1900s historic land use change has been a complicated matrix of habitat destruction and recovery reflecting shifts in agriculture, human development, and resource extraction through time (Sohl et al. 2016). Meanwhile, average annual temperature increased disproportionately in the North and at higher elevations, while precipitation decreased in the Southwest (Gonzalez et al. 2018). Ultimately, impacts on mammal populations have been variable. As expected, many species have declined as their distribution shrank in response to adverse conditions (e.g. many carnivores and ungulates; Laliberte and Ripple 2004). However, others expanded (e.g. coyotes, *Canis latrans*; Hody and Kays 2018), while still others declined and then later recovered (e.g. fishers, *Pekania pennanti*; LaPoint et al. 2015, bobcat, *Lynx rufus*; Litvaitis et al. 2006). In some cases, the precise drivers behind these changes are well documented (e.g., red wolf, *Canis rufus*; Hinton et al. 2013), and such knowledge has proven critical in informing modern conservation and management. However, for many cases, causal mechanisms are uncertain and difficult to ascertain, as exemplified by species like the plains spotted skunk (*Spilogale interrupta*; Gompper and Hackett 2005). In these cases, lack of knowledge regarding suitable habitat, population limiting factors, and links to environmental change create significant challenges for species recovery. Improved understanding of species-specific responses to climate and land-use change is critical to inform current and future species management, particularly in light of ongoing climate and land use change.

Environmental niche models (ENMs) have emerged as valuable tools for understanding the past and future impacts of climate and land use change on species (e.g., Elith and Leathwick 2009; van Beest et al. 2021; Barnes et al. 2022). These models couple species occurrences with environmental data (e.g., climate, land use), enabling the projection of a species' environmental niche and predictions of geographic niche space to past, present, and future landscapes (Elith and Leathwick 2009). For instance, Pease et al. (2009) projected niches of five California deer ecotypes into the last glacial maximum to find that they likely overlapped more than they do today. Zhu et al. (2022) projected niche models of 258 vertebrates into the future to predict species responses to different climate change scenarios and inform conservation efforts. More recently, hindcasted predictions from niche models have leveraged backcasted or historic land use data to test hypotheses and examine the impact of both historic climate and land use change on species (Regos et al. 2018; Cheeseman et al. 2021a). For example, Cheeseman et al. (2021a, b) mapped a century of past changes in suitable habitat for eastern spotted skunk (*S. putorius*) using backcasted climate and land-use data, demonstrating a 37% decline in suitable habitat since 1938 was predicted by changes in land-use and climate. Incorporating hindcasted model predictions over a 30-year period, Regos et al. (2018) similarly found land use change has been an influential driver of change in bird distributions. In both cases, these studies generated hypotheses around drivers of species loss and developed landscape-level habitat suitability maps to evaluate the current distribution of environmentally suitable conditions for the species to guide research and conservation efforts.

In this study, we adopt the approach of Cheeseman et al. (2021a, b) to investigate temporal changes in the environmental suitability for another group of little-known North American mammals of increasing conservation concern – weasels. Three species of weasels are native to the contiguous United States, the American ermine (*Mustela richardsonii*), least weasel (*M. nivalis*), and long-tailed weasel (*Neogale frenata*) (note recent taxonomic name changes; Colella et al. 2021; Patterson et al. 2021). Small bodied and cryptic, little is known about their habitat requirements or population status, and they have never been subject to a large-scale ENM study. Jachowski et al. (2021) recently emphasized the limited knowledge of North American weasel populations and suggested that their numbers may be in decline. Harvest records indicate decreasing trends over time, and patterns of museum specimens and observations suggest that they might now be relatively less common in some regions. However, the absence of systematic survey data makes it difficult to determine the exact status of these species. In the United States, weasels are frequently considered a furbearer and their conservation status varies by species and state, with some considering them Data Deficient (DD) and at least one-third of range states classifying at least one weasel as a species of conservation concern due to their declining populations and limited information (Jachowski et al. 2021). Understanding the climatic and land-use factors affecting these species' distributions is crucial for developing effective conservation strategies.

We created ENMs for the three weasel species to characterize their climatic and land-use niches. We generate annual, time-stepped hindcasted predictive maps of habitat suitability for the contiguous United States from 1938 to 2021 to understand the potential for distributional shifts or range contractions associated with climate and land use change. We evaluated regional trends in total suitable area and the degree of fragmentation in predicted suitable areas, hereafter referred to as niche fragmentation, through time, plotting trends for each species. Given the historic aspects of this study, we defined environmental suitability as the fundamental suite of climate and land use conditions that are consistent with those needed to support life processes of the species but does not consider the geographic or biological barriers that may constrain a species' realized niche (Hirzel et al. 2006). We differentiated environmental suitability from the species distribution, which we considered the true area of extent for a species (Feng et al. 2019). Our results enhanced our understanding of the ecology of these secretive species and provide valuable resources for their conservation.

Methods

We obtained photo-vouchered occurrence records from iNaturalist and museum-vouchered records from the Global Biodiversity Information Facility (www.gbif.org; GBIF.org 2021). We presumed these curated museum specimens, mostly skins and skeletons, were correctly identified to species and only included confirmed iNaturalist records with photos. Additionally, we solicited confirmed species records from state agencies within the North American Weasel Working group. Records were limited to those collected in the contiguous United States between 1938–2021 in order to correspond to the extent and availability of environmental data. Some museum records did not include geographic coordinates but listed a geographic description. For these, we used the Geolocate Web application (https://www.geo-locate.org/) to obtain coordinates and precision estimates from the written location description. For analysis, we retained only those with a coordinate uncertainty <10 km and a record of collection year.

We spatially rarefied records for each species to 10 km to reduce bias due to spatial autocorrelation in sampling of records. Records were thinned using 100 iterations in package 'spThin' in Program R (Boria et al. 2014; Aiello-Lammens et al. 2015; R Core Team 2023). For each species, we constrained the available environmental space used to train the model to a convex hull around each species' occurrence records (Total convex hull area: least weasel = 286 million ha; American ermine = 580 million ha; long-tailed weasel = 972 million ha; Tsoar et al. 2007; Rodríguez-Rey et al. 2019). We then generated 25 randomly selected pseudoabsence points corresponding to each occurrence point from each species' corresponding polygon (Phillips and Dudík 2008).

Environmental data

For each year between 1938 and 2021, we calculated climate and land cover variables thought to influence weasel habitat quality and distribution from available historic and contemporary datasets (Wilson and Ruff 1999). Climate variables temperature isothermality, maximum temperature of the warmest month (hereafter maximum temperature), minimum temperature of coldest month (hereafter minimum temperature), precipitation of wettest month, and precipitation of driest month were obtained at a 4 km resolution from PRISM climate data calculated using the "dismo" package in R v. 4.3.1 (PRISM Climate Group 2014; Hijmans et al. 2023; R Core Team 2023). Climate data were then reclassified to a 10 km resolution and extracted for each occurrence and paired pseudoabsence point by year of observation.

To evaluate the impact of land cover on landscape suitability for weasels, we incorporated land use metrics calculated from backcasted historic (1938–1992; Sohl et al. 2016) and National Land Cover Database (NLCD; 2001, 2004, 2005, 2006, 2008, 2011, 2013, 2015, 2016, and 2019, www.mrlc.gov). NLCD land use data were reclassified to a 250 m resolution to match the scale of backcasted data and facilitate computation. We considered area in farmed agriculture and average cropland patch size as measures of agricultural intensity. Forest cover, represented as the total of mixed, deciduous, and evergreen forest, and shrub cover were included as measures of habitat availability, while Shannon's diversity index and number of patches were included as indicators of landscape diversity and fragmentation (Guerrero et al. 2011; Mineau and Whiteside 2013; Hesselbarth et al. 2019). For each occurrence and pseudoabsense point we calculated these metrics to the nearest year within a 10 km radius of each point using the 'landscapemetrics' package in Program R (mean difference between record and year: least weasel: 0.38 ± 0.80 SD; American ermine: 0.52 ± 0.82 SD; long-tailed weasel 0.46 ± 0.77 SD; Hesselbarth et al. 2019; R Core Team 2023). For all climate and land-cover predictors, we tested for collinearity using Pearson correlations and did not include variables with $r > 0.85$ (Elith et al. 2010).

Modeling approach

We modeled each species' environmental niche using presence and pseudoabsence data and their corresponding time-varying covariates in Maxent 3.4.1 through R packages "dismo" 1.3–14 and "ENMeval" (Phillips et al. 2006; Muscarella et al. 2014; Hijmans et al. 2023). To assess specific model configurations, we executed the global model with various feature class transformations (Linear; Quadratic; Linear and Quadratic; Hinge; Linear, Quadratic, and Hinge) and regularization multipliers (RM: 1.0–5.0 at 0.5 intervals), resulting in 50 distinct models (Anderson and Gonzalez 2011; Guevara et al. 2018). Our primary interest was in predicting temporal shifts in suitability and identifying the variables that influenced it. Therefore, we employed a temporally blocked cross-validation approach for model evaluation, breaking the occurrences and corresponding pseudoabsences evenly into ten chronological training and test blocks based on record years (Roberts et al. 2017). Each test block was subsequently validated against predictions from training block data using environmental and land use/land cover variables corresponding to the mean record year for the test block.

We compared models, inspected them for overfitting and discrimination, and selected a final model configuration for downstream analyses using the threshold-dependent True Skill Statistic (TSS), which measures the difference between omission and commission errors, ranging from -1 to 1 where -1 indicates the model is in perfect disagreement, values of 1 indicate perfect agreement, and 0 indicates performance is no better than random (Velasco and González-Salazar 2019). Additionally, we calculated the threshold-independent method (AUC_{TEST}) and evaluated the ecological context of the top models to evaluate predictive ability (Anderson and Gonzalez 2011; Guevara et al. 2018). AUC values range from 0 to 1 where values from 0.7–0.8 are considered acceptable and values from 0.8–0.9 are considered excellent (Hosmer et al. 2013).

We constructed nine candidate niche models, predefined to represent our hypothesized relationships between weasels and their environments (SI Table 1). These models comprised the global model, a climate only model, and seven models containing subsets of land use/land cover variables from the global model (Table 1). All models included all climate variables. Using the identified configuration settings, we analyzed these models and chose the one with the highest TSS as the final model, also examining AUC_{TEST} and ecological context to assess predictive ability as above.

Using the identified top model for each weasel species, we generated 10-km resolution predictive maps of landscape suitability at all time steps (84 years). To generate landscape rasters for predictions, we calculated variables using the "dismo" package for PRISM climate data and the "lanscapemetrics" package for land use/land cover data, as previously (Hesselbarth et al. 2019; Hijmans et al. 2023). The extent for

Table 1 Model evaluation criteria, mean (SD), based on temporally blocked cross validation of Maxent models. Models contained different landscape variables thought to influence niche suitability for three weasel species in the contiguous United States, 1938–2021

	Least weasel		Long-tailed weasel		American ermine	
	AUC_{TEST}	TSS	AUC_{TEST}	TSS	AUC_{TEST}	TSS
Agriculture, patches, diversity, field size, forest, shrubland, climate	**0.761 (0.058)**	**0.478 (0.114)**	**0.753 (0.068)**	**0.409 (0.102)**	**0.833 (0.027)**	**0.561 (0.043)**
Patches, diversity, forest, shrubland, climate	0.761 (0.06)	0.469 (0.115)	0.752 (0.069)	0.405 (0.107)	0.830 (0.026)	0.553 (0.052)
Agriculture, field size, forest, shrubland, climate	0.742 (0.061)	0.464 (0.112)	0.736 (0.071)	0.388 (0.126)	0.813 (0.028)	0.544 (0.058)
Agriculture, diversity, forest, shrubland, climate	0.755 (0.055)	0.465 (0.110)	0.752 (0.067)	0.406 (0.108)	0.832 (0.027)	0.559 (0.045)
Agriculture, patches, diversity, field size, climate	0.734 (0.071)	0.457 (0.128)	0.746 (0.073)	0.398 (0.115)	0.828 (0.029)	0.555 (0.061)
Patches, diversity, field size, climate	0.732 (0.075)	0.440 (0.123)	0.745 (0.074)	0.398 (0.115)	0.826 (0.030)	0.557 (0.067)
Agriculture, patches, diversity, climate	0.734 (0.070)	0.450 (0.112)	0.745 (0.074)	0.398 (0.115)	0.828 (0.029)	0.555 (0.060)
Agriculture, patches, diversity, field size, forest, shrubland	0.724 (0.068)	0.396 (0.098)	0.692 (0.061)	0.308 (0.097)	0.796 (0.038)	0.492 (0.045)
Climate	0.680 (0.100)	0.353 (0.158)	0.719 (0.076)	0.366 (0.126)	0.800 (0.030)	0.506 (0.060)

predictive maps was limited to the contiguous United States due to the availability of covariate data. For years with no corresponding land use/land cover data (i.e., between years of NLCD dataset availability and between NLCD dataset availability and the availability of hindcasted land use/land cover products, n = 9), we used the nearest year of land use data to correspond with each year's climate data. To provide environmental context for our results, we further quantified how the climate and landscape have changed over time by plotting average climate and landscape data for variables included in top models over four time periods: 1940's, 1950–1969, 1970–1999, 2000–2019 using all pseudoabsence points from each region.

Changes in the distribution and prevalence of suitable conditions and the degree of fragmentation through time were assessed for the contiguous United States and, to aid facilitate regional species management, major U.S. regions (i.e., Northeast, South, Midwest, and West; Bureau of the Census 1994). Specifically, we assessed for changes by using ensembled predictions of cross-validation blocks for both p10 and maxSSS thresholds at each of the 83-time steps (Liu et al. 2013, 2016; van Beest et al. 2021). To assess the degree of niche fragmentation through time, binary thresholded predictions were bounded to the training area (convex hull around presence points) for each species. We then calculated the total area of suitability, average suitable patch area, and edge density of the predicted area of suitability for each species at all time steps using package "landscapemetrics" in Program R (Hesselbarth et al. 2019; R Core Team 2023). We evaluated support for the hypotheses that each weasel species experienced changes in suitable area and niche fragmentation through time by developing a suite of candidate models for each suitable area, edge density, and mean suitable patch size, considering linear and quadratic terms for year and a null model. Candidate model sets were evaluated using a model theoretic approach and Akaike Information Criterion (AICc), and inference made from model averaged predictions (Anderson and Burnham 2004; Cade 2015). Predictions were generated from models using the "modAvgPred" function in the "AICcmodavg" package in Program R (Mazerolle 2023; R Core Team 2023). For brevity, results using the p10 threshold are reported as supplementary material.

Results

After data cleaning and spatial ratification our dataset included 763 American ermine occurrences, 295 least weasel occurrences, and 1,582 long-tailed weasel occurrences (Fig. 1).

Model performance

For American ermine, the best supported model structure included linear, quadratic, and hinge features and a regularization multiplier of 4.0 (TSS = 0.561 SD = 0.043; SI Table 2). TSS was highest for least weasel models including linear, quadratic, and hinge features and a regularization multiplier of 0.5 (TSS = 0.478 SD = 0.114; SI Table 3). For long-tailed weasels, the best supported model structure included linear, quadratic, and hinge features and regularization multiplier of 2.0 (TSS = 0.409 SD = 0.102 SI Table 4). Evaluation of candidate model sets containing hypothesized combinations of land use and climate variables identified the global model containing number of patches, area in agriculture, average field size, landscape diversity, forest cover, shrubland cover, and climate as the best supported model based on TSS and AUC_{TEST} values for all weasel species (Table 1).

Variable importance

For all three weasel species, inclusion of land cover variables improved model performance (Table 2). Forest cover, maximum temperature, and landscape diversity had the highest relative percent contribution and higher permutation importance for American ermine ENMs; all other variables had a relative percent contribution < 5%. Forest cover positively influenced predicted American ermine environmental suitability; at low levels of forest cover the predicted probability of suitability was low, plateaued, then increased to a probability near 1 where forest cover dominated the landscape (Fig. 2). The relationship between predicted probability of suitability for American ermine and landscape diversity exhibited a U-shaped pattern (Fig. 2), possibly reflecting a balance between higher habitat suitability in areas of large intact habitat where land cover diversity is

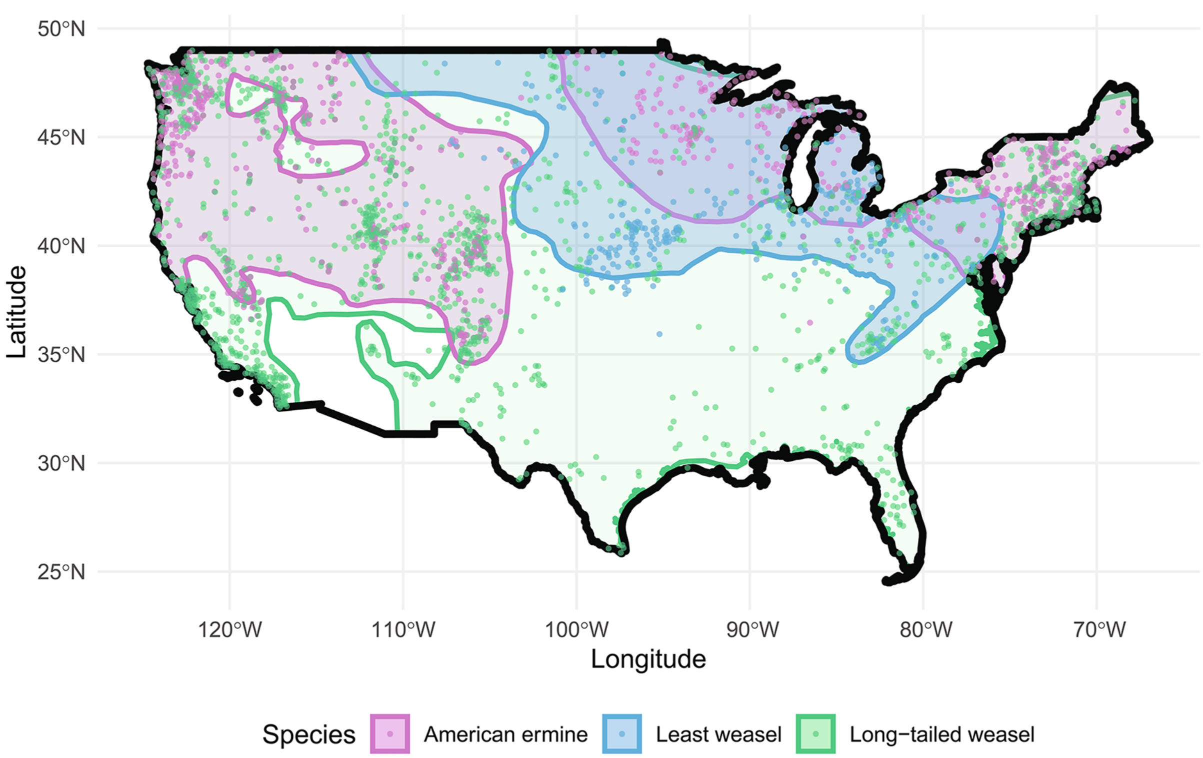

Fig. 1 Occurrence points used in analyses and IUCN range boundaries for American ermine (*Mustela richardsonii*), least weasel (*M. nivalis*), and long-tailed weasel (*Neogale frenata*; IUCN 2021)

Table 2 Variable contribution and permutation importance of variables included in the top environmental niche models for three weasels in the contiguous United States, 1938–2021

	Variable	American ermine		Least weasel		Long-tailed weasel	
		% contribution	Permutation importance	% contribution	Permutation importance	% contribution	Permutation importance
Habitat	Forest cover	40.6	7.2	10.8	16.9	5	4.3
	Agriculture	1.5	3	36.7	3.7	2	2.5
	Landscape diversity	16.6	19.6	2.7	9.6	18.6	27.8
	Number of patches	0.4	2.9	15.9	12	0.4	1.2
	Shrub cover	0.3	0.6	2.8	4.6	5.9	2.7
	Average agricultural field size	0	0	0.8	5.5	0.2	1.9
Total Habitat		**59.4**	**33.3**	**69.7**	**52.3**	**32.1**	**40.4**
Climate	Maximum temperature	37.6	61.1	3.7	6.1	40.1	42.7
	Minimum temperature	2.3	3.6	16.9	29.4	6.7	8.7
	Precipitation in the driest month	0.3	0.8	4.9	4.2	3	2.7
	Isothermality	0.3	0.8	0.9	2	16.2	1.4
	Precipitation in the wettest month	0.1	0.3	3.8	6	1.9	4.1
Total Climate		40.6	66.6	30.2	47.7	67.9	59.6

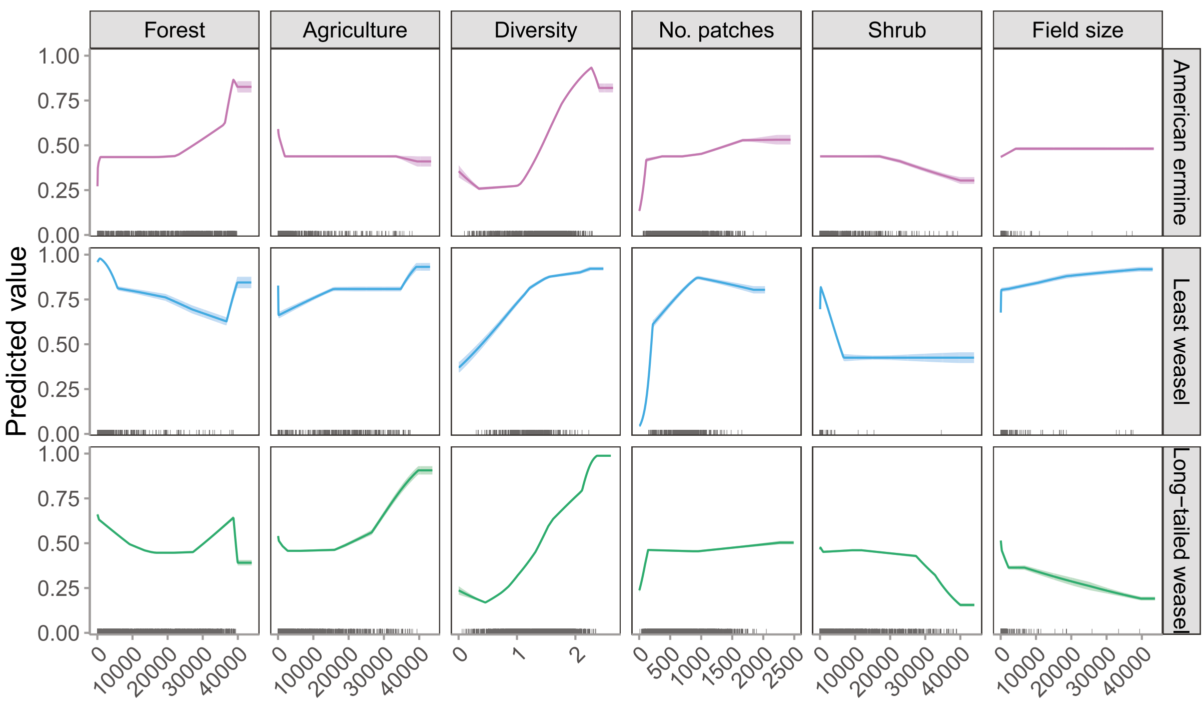

Fig. 2 Response curves (±SE of blocked cross-validation runs) of landscape predictors for environmental niche models for three weasel species in the contiguous United States 1938–2021. Variables include forest cover [ha], Agricultural cover [ha], landscape diversity (Diversity), number of patches, shrub cover [ha], and average agricultural field size [ha]. Observed values for weasel presences noted by rugs along x-axes

low and an otherwise positive association with landscape diversity in fragmented systems (Fig. 3). Lastly, predicted probability of environmental suitability declined for American ermine as maximum temperature increased (Fig. 4), approaching zero where maximum temperatures neared the apparent boundary of this dimension of their Hutchinsonian niche (Fig. 3).

For least weasels, land in agriculture, minimum temperature, number of patches, and forest cover had a relative percent contribution to the model > 5% (Table 2). With the exception of land in agriculture, these variables, alongside landscape diversity, average agricultural field size, and maximum temperature had similarly high corresponding permutation importance values, supporting use in predicting suitable habitat conditions for least weasels. For least weasels, predicted suitability was highest in areas without agriculture; however, where agricultural cover was present, suitability initiated lower and increased with the amount of agricultural cover (Fig. 2). Predicted suitability also increased with both increasing landscape diversity and the number of patches, but only increased with average agricultural patch size along smaller values of this variable (Fig. 2). Relationships between forest cover and predicted suitability were dynamic for least weasels but suggested that peak suitability typically occurred where forests comprised 5–10% of

Fig. 3 Temperature (left) and habitat (right) niches for three weasel species in the contiguous United States (1938–2021). Dots show the conditions actually used by weasels during the corresponding year of their observation

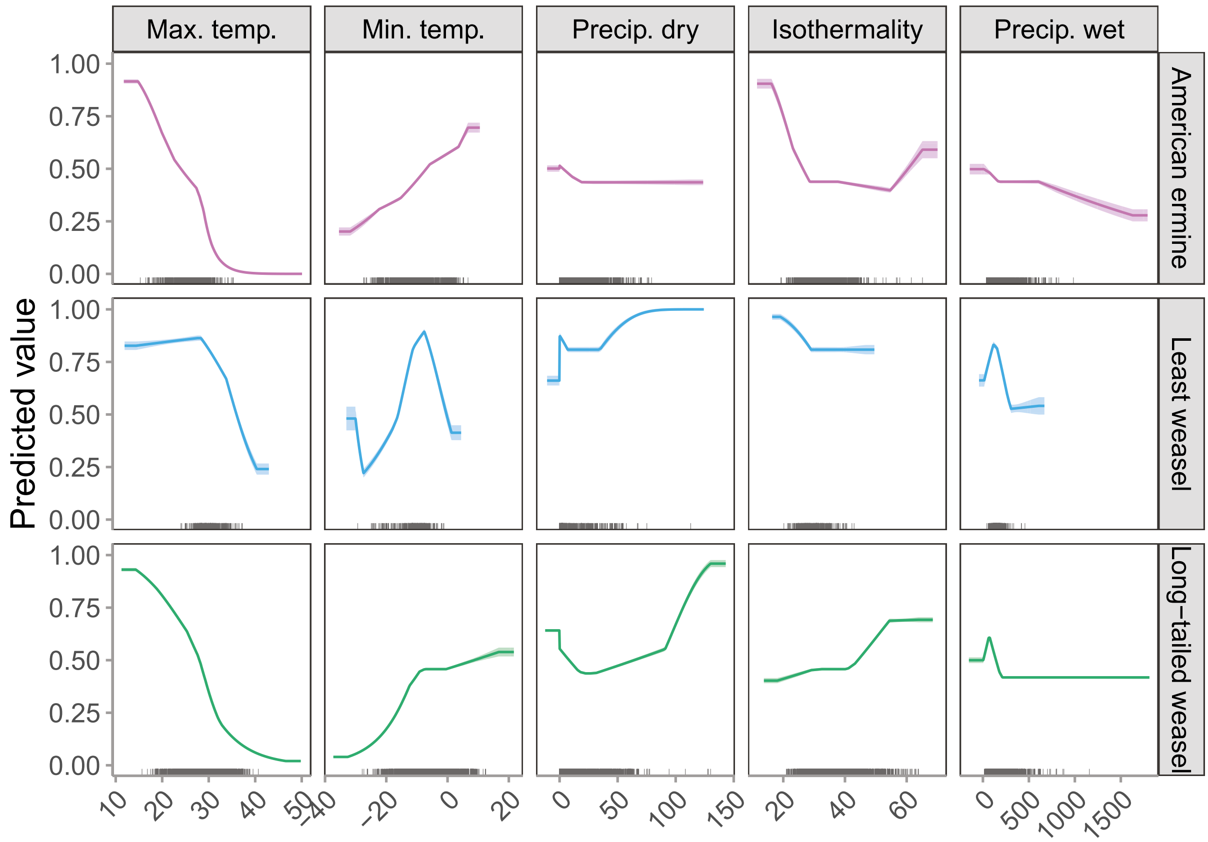

Fig. 4 Response curves (±SE of blocked cross-validation runs) of climate predictors for environmental niche models of three weasel species in the contiguous United States (1938–2021). Variables include maximum temperature of the warmest month (Max. temp.) [°C], minimum temperature of the coldest month (Min. Temp.) [°C], precipitation of driest month (mm), temperature isothermality, and precipitation of the wettest month (mm). Observed values for weasel presences noted by rugs along x-axes

the landscape (Fig. 2). Suitability may also increase for large tracts of intact forest; however, interpretation may be hindered by the limited occurrence of these forests within the distribution of least weasels examined. Similar to American ermine, there appeared to be a tradeoff between increased suitability with higher levels of landscape diversity and higher habitat suitability in areas of large intact forests (Fig. 3). Predicted suitability was hump shaped across values of minimum temperature of the coldest month suggesting narrow winter-season thermal tolerances are related to suitable environments for least weasels (Fig.); a notion further supported when plotting the temperature dimensions of their Hutchinsonian niche (Fig. 3). Again, similar to American ermine, predicted suitability declined with increasing maximum temperature; however, unlike American ermine, predicted suitability remained above 0% at the upper bound of maximum temperature (Fig. 4).

Long-tailed weasel habitat suitability appeared to be influenced by maximum temperature, landscape diversity, isothermality, minimum temperature, shrub cover, and forest cover as the relative percent contribution of these variables was > 5%. However, only landscape diversity, maximum temperature, and minimum temperature had similarly high permutation importance (Table 2). Landscape diversity showed a u-shaped response similar to American ermine (Fig. 2), likely reflecting tradeoffs between moderate predicted suitability in intact tracts of habitat and increasingly high predicted suitability with higher levels of landscape diversity (Fig. 3). Similar to American ermine and least weasels, predicted suitability for long-tailed weasels decreased with increasing maximum temperature (Fig. 4). However, long-tailed weasel environmental suitability declined less rapidly with increasing temperature, reflecting their wider range of suitable temperatures when compared to American ermine (Fig. 3). For the minimum temperature of the coldest month, predicted suitability increased rapidly with increasing temperatures and plateaued around -10 °C.

Environmental change

We plotted regional landscape data over time to see how the most important covariates for weasel ENMs changed in different regions. We found that forest cover generally increased in the Northeast until recently but was continuously lost in the West (Fig. 5). For landscape diversity, gradual increases in the West ended with a steep decline after the 1990s, while in the Northeast recent increases marked the end of a gradual decline in landscape diversity over the past century. Maximum and minimum temperature have increased over the past few decades in both the Northeast and West. A warming trend was also seen in the last 20 years in Midwest and South, although forest cover and landscape diversity has been less dynamic in these regions (SI Fig. 1).

Complex changes in the distribution of suitable habitats for North American weasels reflect these regional changes in land use and climate. For American ermine, present day areas of high predicted habitat suitability occurred within Northern areas of the

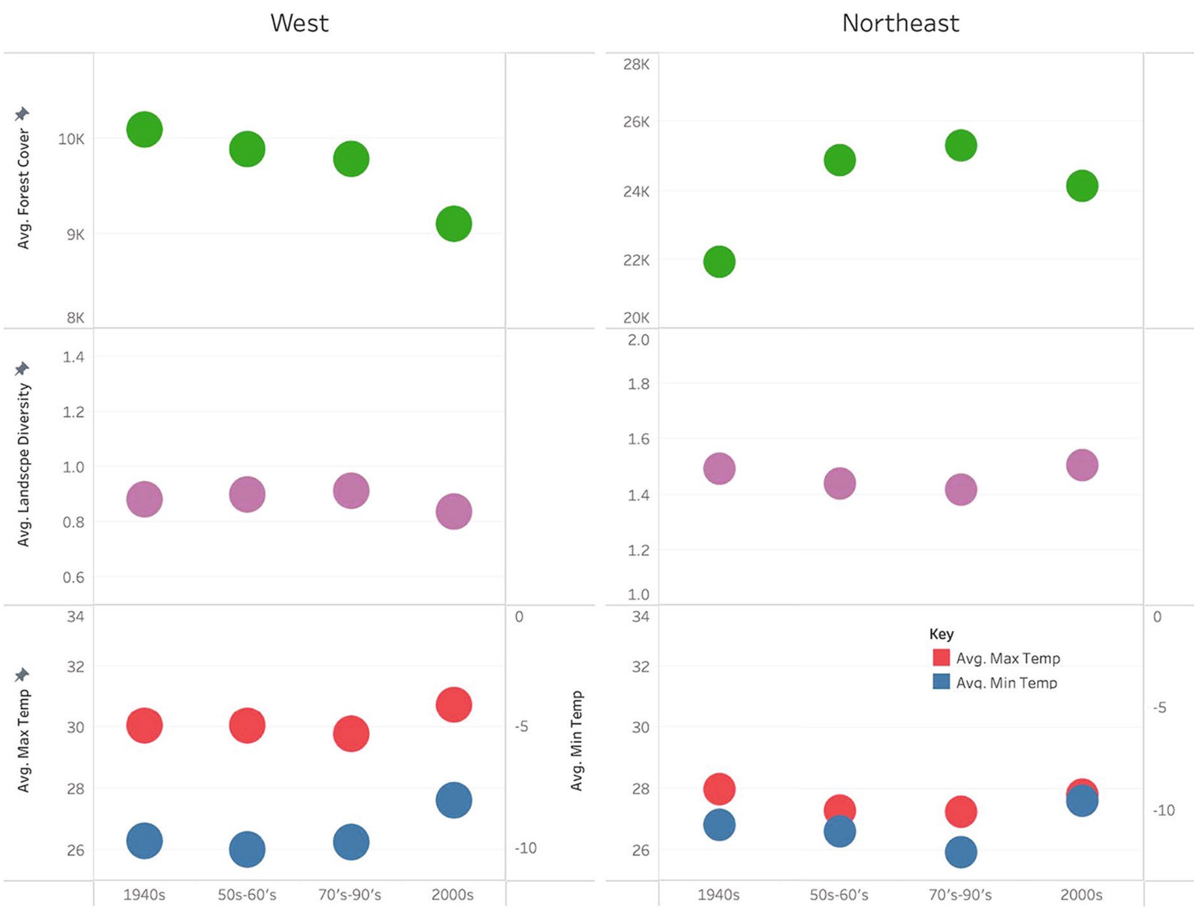

Fig. 5 Change in habitat and climate over time in two regions of the contiguous United States (1938–2021). Variables include forest cover [ha], landscape diversity (Diversity), maximum temperature of the warmest month (Avg. Max Temp, red) [°C], and minimum temperature of the coldest month (Avg. Min Temp, blue) [°C]

Northeast, Northeastern Midwest, and at higher elevations in the Rocky and Cascade Mountain ranges (Fig. 6). Relatively little area within their geographic range fell in the South. The geographic distribution of present suitable conditions was the product of a predicted initial expansion in the area of predicted suitability of 9% (10.64 million hectares) between 1938 and 1981 and more recent contractions (loss of 9.06 million ha since 1981, Fig. 7, model selection results reported in SI Table 5); however, confidence intervals on these predictions were large. Expansions in predicted suitable conditions for American ermine occurred in the Northeast, Midwest, and South, representing increases of 35%, 37%, and 133% since 1938, respectively (8.73, 8.94, and 3.27 million hectares, respectively; Fig. 7). Recent declines in suitable conditions for American ermine were concentrated in the West after peaking in 1966 and represent a 31% (19.01 million hectares) loss from 1938 baselines (Fig. 7). These predicted declines were most apparent at lower elevations and more southern areas of the Rocky and Cascade mountain ranges (Fig. 6). Trends toward increased or decreased niche fragmentation largely corresponded to contractions or expansions in suitable conditions, respectively, for American ermine (Fig. 7). Overall, average suitable patch area decreased by 42% (0.47 million hectares) after 1968 (Fig. 7), but changes in the edge density of suitable conditions for American ermine were minimal between 1938 (0.02 ± 0.001 SE) and 2021 (0.02 ± 0.001 SE). Increased fragmentation of suitable conditions in the West was suggested by a 43% increase in edge density after 1966 and corresponding decreases in average suitable patch area totaling 63% (0.63 million hectare) since 1965. Meanwhile, suitable conditions may have become less fragmented in the Northeast and South since the mid the twentieth century (i.e. 1946 and 1955, respectively) as indicated by decreases in edge density (33% and 20%, respectively), and increased suitable patch area in the Northeast (221%, 4.93 million hectares; Fig. 7). Predicted trends in suitable patch area for American ermine also suggested an increase of 35% (0.11 million hectares) in the South; however, the confidence intervals

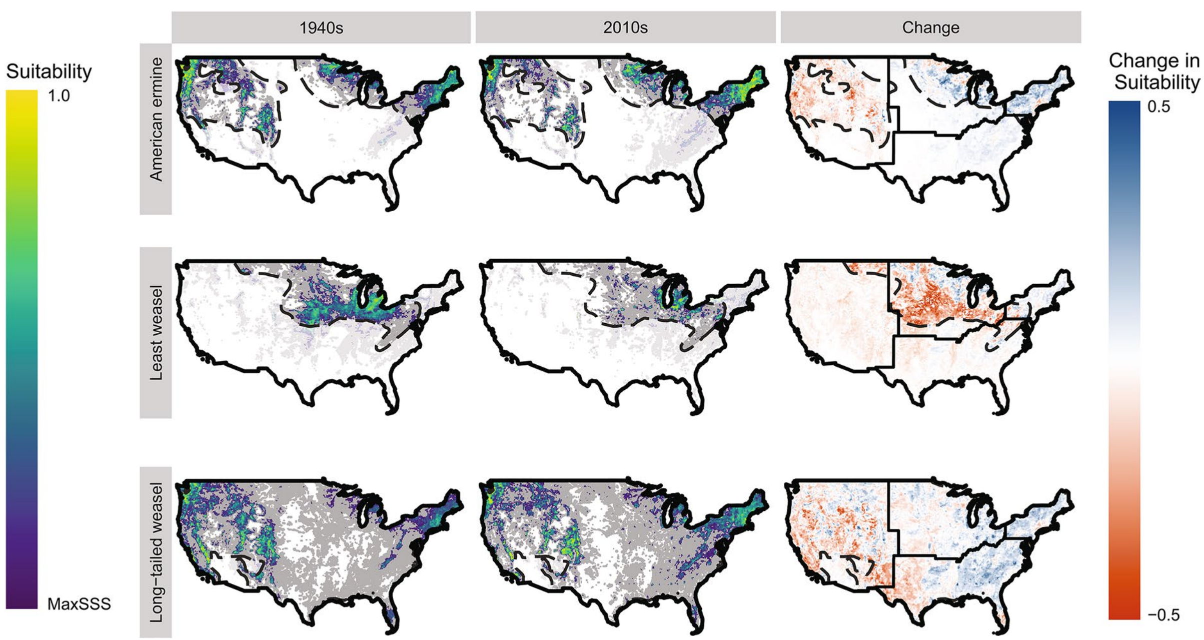

Fig. 6 Predicted distribution of suitable conditions for three weasel species in the contiguous United States in the 1940s (calculated as mean of 1940–1949 predictions) and 2010s (calculated as mean of 2010–2019 predictions) based on the p10 (gray area) and MaxSSS thresholds (viridis color scaling where purple is low suitability and yellow indicates high suitability). The difference in predicted suitability between 1940 and 2010s predictions (blue indicates areas where suitability increased, red where suitability decreased) and major United States regional boundaries (thick black line) shown in the right column. Areas falling outside IUCN Red List species range boundaries (dashed line) are shaded (IUCN 2021)

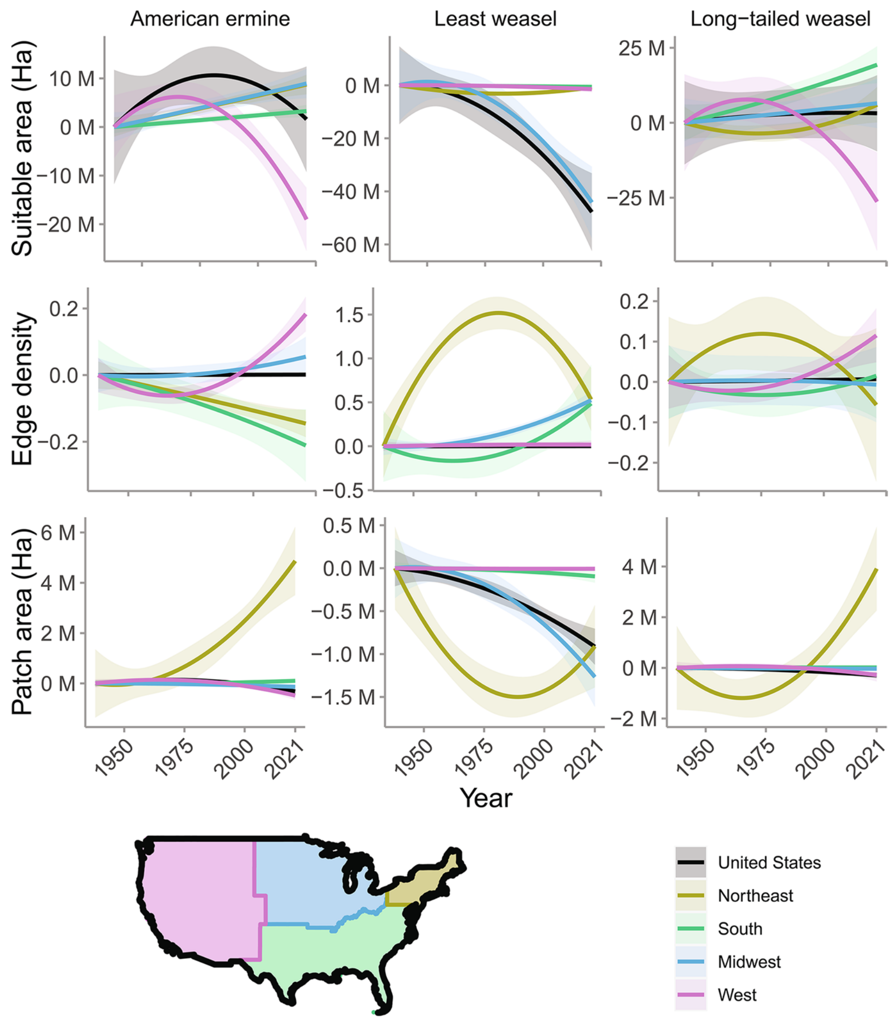

Fig. 7 Change in annual predictions of suitable area and fragmentation indices (95% confidence intervals shown) from 1938 baselines for three weasel species in the contiguous United States and major regions (1938–2021). Predictions generated at the MaxSSS threshold and bounded to the geographic range of each species

on these predictions were large (1938: 0.18 ± 0.03; 2021: 0.08 ± 0.04; Fig. 7). Metrics of fragmentation in the Midwest suggested increased fragmentation of suitable areas for American ermine during the twentieth century, despite gains in predicted area of suitability. Here, edge density of suitable areas increased by 10% after 1955 while average suitable patch area decreased by 19% (0.14 million hectares; Fig. 7).

Suitable conditions for least weasels were historically concentrated in the southern Midwest with small pockets in other regions (Fig. 6). However, the prevalence of suitable conditions declined after 1938, resulting in a 54% loss of suitable conditions and including the widespread loss and fragmentation of suitable conditions for least weasels in all but the lower peninsula of Michigan and eastern Wisconsin, USA (Fig. 6, model selection results reported in SI Table 6). Predicted declines at the core of the least weasel range in the Midwest occurred after an initial predicted increase of 1.31 million hectares between 1938 and 1950 and represent a 57% loss from 1938 baselines (44.16 million hectares; Fig. 7). Suitable areas overall and Midwest both showed evidence of fragmentation as average suitable patch area decreased 80% (0.91 million hectares) and 88% (1.28 million hectares), respectively, while edge density increased by 144% in the Midwest (Fig. 7). Changes in the overall edge density of predicted suitable areas for least weasels were negligible (1938: 0.01 ± 0.005 SE to 2021: 0.01 ± 0.001 SE). In the Northeast, West, and South the distribution of suitable conditions for least weasels remained limited through time (Fig. 6). In the Northeast, the prevalence of suitable conditions initially declined 80% (3.17 million hectares) between 1938 and 1982 but has started to increase more recently (2.41 million hectare increase since 1982). Indices of niche fragmentation for least weasels in the Northeast inversely mirrored patterns in suitable conditions, indicating a substantial increase in fragmentation corresponding to losses in potentially suitable habitat followed by a decrease to present day. Predicted suitable patch area in the Northeast initially declined by 92% (1.50 million hectares) until 1989 but increased by 0.59 million hectares since (Fig. 7). Similarly, edge density of suitable conditions for least weasels in the Northeast increased by 504% until 1984, but then declined to 176% of the edge density predicted in 1938 (Fig. 7). Trends in suitable conditions in the South and West were suggestive of declines from the 1938 baseline; however, confidence bounds on predictions were large (South 1938: 3.59 ± 0.66 SE, 2021: 2.98 ± 0.69 SE; West 1938: 3.30 ± 0.58 SE, 2021: 1.84 ± 0.58 SE). However, the edge density of suitable areas in the South increased 46% after 1966. Point estimates for trends in suitable patch area in the South declined between 1938 and 2021 but 95% confidence intervals on predictions were large (1938: 0.17 ± 0.66 SE million hectares to 2021: 0.08 ± 0.69 SE, respectively; Fig. 7). Predicted changes for indices of fragmentation in the West were negligible, suitable patch area decreased from 0.19 ± 0.58 SE million hectares in 1938 to 0.18 ± 0.58 SE million hectares in 2021, while edge density of predicted suitable areas for least weasels increased from 1.22 ± 0.03 SE in 1938 to 1.24 ± 0.02 SE in 2021 (Fig. 7).

For long-tailed weasels, suitable conditions were concentrated in the Northeast and West with a fragmented distribution of suitable areas in the Midwest and South. Overall, the prevalence of suitable conditions increased 2% (3.32 million hectares) between 1938 and 2006, followed by declines of 0.16 million hectares between 2006 and 2021; however, the 95% confidence bounds on predictions were large at this scale (model selection results reported in SI Table 7). At regional scales, increases in the distribution of suitable conditions were confined to the southern Appalachians and small fragmented patches across the South (142% and 19.34 million hectare increase; however, note localized declines in South Florida), Midwest (27% and 6.49 million hectare increase), and Northeast after initial declines reversed in this region after 1969 (9.58 million hectare increase since 1969 and 20% increase or 6.02 million hectares since 1938, Fig. 7). These gains represented a southern expansion of suitable conditions in the Northeast and Michigan as well as increased suitability along the southern Appalachian Mountains (Fig. 6). While eastern portions of the contiguous United States saw expansions of suitable conditions for long-tailed weasels, the prevalence of suitable conditions in the West declined from a peak in 1965, representing a loss of 23% in predicted suitable area from the 1938 baselines (26.33-million-hectare loss; Fig. 7). Similar to American ermine, these losses appeared to be concentrated in southern regions and at lower elevations in the Cascade and Rocky Mountain ranges (Fig. 6). Despite increases in the total amount of predicted suitable habitat, suitable areas for long-tailed weasels may have become more fragmented. Overall, average suitable patch area declined by 32% (28.94 million hectares), while edge density increased by 20% (Fig. 7). These findings were reflected in the West where average suitable patch area increased by 6.93% between 1938 and 1964 then decreased 29% (0.27 million hectares) from 1938 baselines by 2021 (Fig. 7). Similarly, point estimates suggested edge density of suitable areas in the West initially decreased until 1962 (predicted 1962 edge density = 0.52 ± 0.01 SE) then increased for long-tailed weasels, representing a 21% increase from the 1938 baseline (predicted 1938 edge density = 0.54 ± 0.03 SE) by 2021 (predicted edge density = 0.65 ± 0.03 SE); however, the 95% confidence bounds on predictions were large relative to the magnitude of the trend (Fig. 7). Northeastern trends were similar to those seen for American ermine; fragmentation increased through the mid-1960s-1970s as demonstrated by 32% (1.19 million hectares) decrease in average suitable patch area and a 34% increase in edge density between 1938 and 1965 and 1975, respectively (Fig. 7). Since then, average suitable patch area increased 106% (3.91 million hectares) from 1938 baselines by 2021, while edge density decreased past historic levels, representing a 16% decrease in edge density from the 1938 baseline (Fig. 7). In the South, model predictions for fragmentation indices had large 95% confidence intervals, but suggested suitable patch area declined until 2008 (predicted 2008 patch area = 0.29 ± 0.02 SE million hectares) then recovered to near 1938 baselines (predicted 1938 patch area = 0.28 ± 0.03 SE million hectares) by 2021 (predicted 2021 patch area = 0.29 ± 0.02 SE million hectares) (Fig. 7). Edge density of predicted suitable areas for long-tailed weasels in the South initially increased 5% until 1976 (predicted 1976 edge density = 0.87 ± 0.03 SE) then decreased to represent a 2% increase over 1938 baselines (predicted 1938 edge density = 0.90 ± 0.05 SE) by 2021 (predicted 2021 edge density = 0.92 ± 0.05 SE; Fig. 7). Similarly, model predictions for fragmentation indices in the Midwest had large 95% confidence bounds on predictions. Point estimates for average suitable patch area steadily decreased by 8% (0.03 million hectares) between 1938 (predicted 1938 patch area = 0.41 ± 0.03 SE million hectares) and 2021 (predicted 2021 patch area = 0.38 ± 0.04 SE million hectares; Fig. 7). Changes in edge density of suitable areas for long-tailed weasels were negligible between 1938 (0.89 ± 0.05 SE) and 2021 (0.88 ± 0.05 SE; Fig. 7).

Discussion

Climate and land use have changed dramatically in the last century, but rarely have we been able to evaluate the relative importance of these on habitat suitability for wildlife. Here we extend recent advances in habitat reconstruction and species distribution models to characterize suitable habitat for three weasel species that are declining in parts of their range and show how these have changed since 1938. Our analyses highlighted the widespread loss and fragmentation of suitable conditions for least weasels during the last century. We noted diverging regional trends for American ermine and long-tailed weasels where patterns of decline and fragmentation of suitable conditions dominate the West while increases in suitable conditions were notable in the eastern United States.

In particular, temperature appears to be a critical determinant of habitat suitability for North American weasels. For least weasels, suitability declined with lower values of minimum temperature. While the northernmost areas of the least weasel's geographic range were not a focus of this study, it may be that as the smallest member of the weasel family examined here, tradeoffs between body size and energetic requirements of thermoregulation in cooler climates play a larger role in limiting the suitability of colder habitats for least weasels than for other weasel species (Blackburn and Hawkins 2004; Zub et al. 2009). In contrast, warm temperatures appeared to limit the southern and lower elevation ranges of all weasel species. Declines in the distributions of suitable conditions for American ermine and long-tailed weasels occurred primarily within the warmer southern and lower elevation regions, with declines more severe in the western United States. For least weasels, declines in predicted suitable conditions were similarly most severe along their southern range boundary. The observed inverse relationship between maximum temperature and habitat suitability for American ermine and long-tailed weasels, alongside the least weasel's intolerance to high minimum temperatures, posits climate change as a potential driver of observed losses and indicates the potential for further range contractions in these areas as the climate warms. These findings are consistent with the southern and low elevation range contractions observed in many climate-impacted species in the Northern hemisphere (Chen et al. 2011; Zimova et al. 2014; Ferreira et al. 2023). As small bodied mammals with a high surface-to-volume ratio, thermoregulatory requirements in cool climates may bring weasels close to physiological limits (Zub et al. 2009). Weasels mitigate temperature extremes by using subnivean microhabitats (Zub et al. 2009); however, declines in persistent snow cover as a result of climate change may limit their ability to reduce physiological demands in cool climates through microhabitat selection, contributing to reduced fitness and range contractions in colder areas of inconsistent snowpack. Further, decreased winter survival associated with camouflage mismatch due to increasingly inconsistent snow cover has been widely proposed to explain low latitude and low elevation range contractions in species with distinctive seasonal molts, including weasels (Atmeh et al. 2018). This camouflage mismatch hypothesis is consistent with the mid-latitude and low-elevation losses presented herein. However, populations of long-tailed weasels and American ermine that occur in more temperate areas of no or inconsistent snowpack, such as the southern United States and Pacific Northwest do not undergo distinctive seasonal molts (Hall 1951; Mills et al. 2018; Davis et al. 2019; Miranda et al. 2021; Harty and Stains 2022). In these regions, camouflage mismatch is unable to explain observed range contractions.

Large scale land use change has also altered the distribution and connectivity of suitable conditions for North American Weasels. The trends in forest cover observed here were consistent with wider findings of land use change reported for the United States. In particular, large-scale agricultural abandonment during the mid-twentieth century and subsequent forest regeneration resulted in large increases in forest cover in the Northeastern United States through the late 1900s (Litvaitis 1993). However, declines in Northeastern forest cover in the past few decades are beginning to reverse this trend (Adams et al. 2019). In forested areas of the western U.S., climate, disease, pests, and forest fire resulted in more recent (post 1970) declines in forest cover, consistent with our findings here (Sleeter et al. 2013; Sohl et al. 2016). While few studies have examined the habitat needs of North American weasels, American ermine have a noted association with forests, though use of grassland, shrubland, and meadows has also been recorded (Lisgo 1999; Linnell et al. 2017; Evans and Mortelliti 2022). We also noted forest cover positively influenced suitability for this species, and regions (e.g., Northeast) that gained forest cover showed corresponding increased suitability while areas that lost forest cover (e.g., Rocky Mountain and Pacific Northwest; Sleeter et al. 2013; Sohl et al. 2016) showed similar declines in the area of predicted suitability.

While American ermine appears to be associated at broad scales with forested landscapes, least weasels tend to avoid forest cover at landscape scales (Zub et al. 2008). Instead, this species is more commonly associated with more open habitat such as grasslands, meadows, and residual edge features within an agricultural matrix (Polder 1968; Macdonald et al. 2004; Zub et al. 2008; Magrini et al. 2009). Our study similarly observed suitability for least weasels decreased across the range of forest cover typically observed across their distribution but may have slightly increased with the amount of land in agriculture. We also noted an increase in suitability with the number of land cover patches. Midwestern landscapes are the result of a complex history of local cropland expansion during favorable periods and subsequent contraction (Sohl et al. 2016). Ultimately, native grasslands have been lost throughout much of the region while agricultural intensification is associated with the replacement of small, diversely planted croplands with large single-crop fields and a reduction in the amount of favorable edge habitat for many species (Samson et al. 2004; Askins et al. 2007; Raven and Wagner 2021). This transition in farming techniques has already been implicated in the decline of a sympatric mesocarnivore, the plains spotted skunk (Gompper and Hackett 2005; Cheeseman et al. 2021b). Together, the positive association with patch number and agriculture for least weasels suggests that similar to plains spotted skunk, in agriculturally dominated landscapes, the interspersion of other land cover classes and associated edges may be needed to support least weasels.

Long-tailed weasels, with the widest distribution of any weasel in the western hemisphere, are the least specialized of the three species examined (Ruiz-Campos et al. 2009). While some studies have suggested a positive association with forested environments, grasslands, or edge habitats (Polder 1968; Sheffield and Thomas 1997), Gehring et al. (2021) noted habitat selection of long-tailed weasels does not differ from the assumption of random use at landscape scales. Likewise, Evans and Mortelliti (2022) found no relationship between forest cover and long-tailed weasel occupancy, suggesting reported variability in habitat associations for this species may be due to their large geographic distribution. We also found that neither forest cover, nor any other land cover class was a strong predictor of suitable conditions for long-tailed weasels.

Landscape diversity, however, is commonly associated with positive outcomes for generalist carnivores (Oehler and Litvaitis 1996; Pita et al. 2009; Güthlin et al. 2013; Heim et al. 2019), such as American ermine and long tailed weasels. Consistent with this generalization we also found positive associations between landscape diversity and American ermine and long-tailed weasel habitat suitability and marginal evidence for this association in least weasels. Edge features, landscape disturbance, and landscape mosaics have all been identified as important habitat features for weasels (Polder 1968; Magrini et al. 2009; Evans and Mortelliti 2022). For example, while forest does not appear to be a strong predictor at landscape scales for long-tailed weasels, at smaller scales Gehring et al. (2021) noted selection for edge features such as fencerows and drainage ditches, as well as forest cover in agriculture dominated landscapes. In forest dominated environments, Evans and Mortelliti (2022) found the probability of occupancy increased with the amount of forest disturbance on the landscape for both long-tailed weasels and American ermine. In both studies, weasel habitat use was thought to be driven by access to abundant prey associated with edge and early successional features. We suggest the u-shaped relationship between suitability and landscape diversity reflects a balance between higher suitability in areas with large intact tracts of habitat where land cover diversity is low, and an increasing benefit as more land cover types increase the amount of edge habitat, provide disturbances in intact landscapes, and otherwise create landscape mosaics that provide access to diverse prey sources.

Carnivores, which often have large area requirements and occur at low densities, may be particularly sensitive to the effects of habitat fragmentation (Purvis et al. 2000). Weasels, as smaller bodied carnivores may additionally perceive their landscape at a smaller scale intensifying the negative effects of landscape fragmentation (Gehring and Swihart 2003). Consistent with this, fragmentation of suitable habitats has been linked with higher predation rates, lower population viability, and lower vagility in weasels (Crooks 2002; Gehring and Swihart 2003, 2004). We note climate and land use change have contributed to a general trend toward higher niche fragmentation today than historically for all weasel species. Such trends may make populations more vulnerable to decline as large tracts of suitable habitat continue to be fragmented into smaller, isolated patches containing fewer individuals (Willi et al. 2006; Oliver and Morecroft 2014). Moreover, niche fragmentation can limit species' ability to shift or adapt to changing environmental conditions as population size is reduced and movement is limited by the intervening matrix (Oliver and Morecroft 2014). Preserving population connectivity may be of particular concern for weasels as adaptation to climate change may hinge on preserving gene flow between populations with and without seasonal coat change.

Our models, producing hindcasted predictions of environmental niche for North American weasels may help to elucidate trends in these otherwise cryptic and poorly understood species. These models predict the area of environmental suitability based on input variables across a defined extent, yet do not explicitly consider external factors such as dispersal abilities or interspecific interactions that may limit the realized niche of a species (Sinclair et al. 2010). For example, these models predicted areas external to the recognized range of modeled weasel species (grayed out Fig. 6, not considered in modeled calculations), as well as substantial loss and recovery of niche space in regions such as the Northeast. Whether these regions are or are not occupied depends on the unknown colonization abilities of individual species. As we modeled and considered change within their currently defined distribution, our results explicitly represent predicted suitability and change in suitable conditions across this area. Environmental niche models also assume species response to their environment is static through time. Adaptation to changing environmental conditions can alter species response to modeled covariates and may result in inaccurate predictions; however, studies of evolutionary change have emphasized high rates of niche conservatism, particularly over geologically short time spans, such as examined here (Peterson 2011). Further work regarding movements, space use, and landscape dynamics of weasels could greatly enhance our understanding of weasel response to landscape change and enable their consideration in future ENMs. In particular, models accounting for local adaptation, particularly for the wide-ranging long-tailed weasel could tailor inference to particular population segments of conservation interest, such as those in the southeastern United States. As we demonstrate North American weasels may be highly susceptible to both climate and land use change, future ENMs consider local adaptation alongside movement abilities of weasels and forecast responses to future environmental change could greatly benefit species managers.

Currently, weasels are most commonly managed as harvestable furbearers in the United States, which could contribute to their decline. While listed as uncommon (S3) at the southern boundary of their western range, American ermine are largely unprotected from harvest in western states where we note suitability has declined. Least weasels, which lost suitable habitat rangewide, are generally recognized as species of conservation concern along their eastern range boundary, but not in the western half of their range, where we found habitat suitability has also greatly decreased. Conversely, while our models suggest western declines of long-tailed weasels, the consideration of long-tailed weasels as a species of concern demonstrates no clear pattern in all regions but the South, where they are listed as a species of concern in most states, but where our models did not identify many areas of high suitability or declines.

One possibility is that the South does not contain much high-quality habitat and as a result, long-tailed weasels have always occurred at low density; however, this is not supported by high historic harvest from this region (Jachowski et al. 2021). Another possibility is North American weasels face multiple threats. Secondary poisoning from rodenticides, increase in predator populations, overharvest, and disease have been implicated alongside land use and climate to describe declines of North American weasels, and may present particular concern where population declines are recognized but no substantial change in environmental suitability is recognized (Jachowski et al. 2021).

Conclusions & management recommendations

Recent studies have suggested population declines in North American weasels, yet a lack of information regarding population status and trends presents a major factor limiting effective management of these species (Jachowski et al. 2021). Our study, the first to develop comprehensive, large-scale ENMs for three North American weasel species, tracks historic changes in suitability highlighting climate and land use changes as potential drivers of regional declines, culminating in modern-day predictions of environmental suitability to focus for future survey and management efforts.

We identified shared recurring themes about the importance of habitat and climate that may be considered in future species management. If the region's climate continues to warm, weasel populations may face continued challenges for persistence along their southern and lower elevation boundaries. Landscape management to reduce habitat fragmentation in areas of concern and facilitate movement and gene flow will be critical to help weasels track suitable conditions and persist in these warming regions. Of particular concern should be the predicted loss of nearly 54% of suitable habitats for least weasels. Declines in least weasel populations have received increasing attention by state wildlife managers, particularly in their eastern range (Jachowski et al. 2021). We found declines may be larger scale than presently realized and populations may warrant additional conservation actions to prevent further decline. Least weasels will likely benefit from landscapes that maintain more diverse land cover classes and associated edges. As suitable areas for least weasels in the contiguous United States are largely in agriculturally dominated landscapes, continued agricultural intensification and land use conversion in the Midwest should be of concern for their management. For American ermine, we found that diverse forest cover is important, providing a clear habitat management recommendation. In contrast, long-tailed weasels can survive in a variety of habitats yet still showed a potential sensitivity to warming climates. Management for long-tailed weasels may benefit from reducing fragmentation of suitable areas and maintaining a diversity of land cover classes. For all species, new monitoring efforts are greatly needed to assess current population status, test predictions of environmental niche, and evaluate the importance of other factors that might be contributing to their decline such as rodenticides, predators, harvest, or disease.

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Data availability The datasets analyzed during the current study and output distribution raster files are available in the Open PRAIRIE repository (https://openprairie.sdstate.edu/nrm_datasets/15).

Declarations

Competing interests The authors declare no competing interests.

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