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Research article

Snow limits polecat *Mustela putorius* distribution in Sweden

Thomas Osinga[1], Henrik Thurfjell[2] and Tim R. Hofmeester[1]

[1]Dept of Wildlife, Fish and Environmental Studies, Swedish Univ. of Agricultural Sciences, Umeå, Sweden
[2]Swedish Species Information Centre, Swedish Univ. of Agricultural Sciences, Uppsala, Sweden
Correspondence: Thomas Osinga (Thomas.osinga@outlook.com)

Many species show range expansions or contractions due to climate change induced changes in habitat suitability. In cold climates, many species that are limited by snow are showing range expansions due to reduced winter severity. The European polecat *Mustela putorius* occurs over large parts of Europe with its northern range limit in southern Fennoscandia. However, it is to date unknown what factors limit polecat distribution. We thus investigated whether climate or land-use variables are more important in determining the habitat suitability for polecats in Sweden. We hypothesized that 1) climatic factors, especially the yearly number of snow days, drive habitat suitability for polecats, and that, 2) as the number of snow days is predicted to decline in the near future, habitat suitability in northern Sweden will increase. We used a combination of sightings data and a selection of national maps of environmental factors to test these hypotheses using Maxent models. We also used maps of future climate predictions (2021–2050 and 2063–2098) to predict future habitat suitability. The number of snow days was the most important factor, negatively determining habitat suitability for polecats, as expected. Consequently, the predictions showed an increase in suitable habitat both in the current distribution range and in northern Sweden, especially along the coast of the Baltic Sea. Our results suggest that the polecat distribution is limited by snow and that reduced snow cover will likely result in a northward range expansion. However, the exact mechanisms for how snow limits polecats are still poorly understood. The potential range expansion might result in a population increase of the Scandinavian polecat population, in contrast to many populations elsewhere in Europe, where numbers are declining. Due to polecat predation, the expansion of the species might have cascading effects on other wildlife populations.

Keywords: climate change, habitat suitability, Maxent, Mustelidae, snow cover

Introduction

Habitat and climatic variables are driving factors of species distributions (Hirzel et al. 2006, Balestrieri et al. 2016). A rapidly changing climate and increased human impact on the global environment has changed the suitability of habitat for many species (Troia et al. 2019). As a consequence, species are showing range expansions and

contractions (Mccain and King 2014, Pacifici et al. 2020). Ranges of species that are limited by cold conditions are moving, shifting to higher elevation or towards the poles, as climates become more favourable due to climate change (Guralnick 2007, Loarie et al. 2009). Such range expansions are well studied in several taxonomic groups such as plants, insects and birds (Thomas and Lennon 1999, Robinet and Roques 2010, Hampe 2011). However, such studies of wild mammals are relatively rare (but see Lundy et al. 2010), partly because they are harder to study and perhaps because their responses to a changing climate might be less pronounced.

Habitat suitability modelling allows the study of factors determining the distribution of wild mammals (Guisan and Zimmermann 2000). These models use presence–absence or presence-only data of species observations to find associations between habitat or climatic factors and species presence to predict the suitability of habitat at larger geographical scales (Zielinski et al. 2010). Furthermore, these models can be used to predict future habitat suitability if future projections of key factors exist (Elith and Leathwick 2009). These models thus use the habitat selection of a species at large geographical scales (1st order of selection sensu Johnson 1980) to predict (potential) species distributions. Note that this is a different spatial scale compared to the distribution of individuals over a landscape (2nd order) or the selection of certain habitat types over others by individuals (3rd order). Habitat suitability models have become very popular due to the accessibility of the Maxent software (Phillips et al. 2004, 2006). However, care has to be taken when interpreting model results, as models predict where a species could potentially occur based on its climatic and habitat niche, which does not necessarily represent its actual distribution (Moreno-Amat et al. 2015). Nevertheless, these models are very suitable to explore which factors determine the distribution of species and how those distributions might potentially change under future scenarios.

The European or western polecat *Mustela putorius* L. occurs in large parts of Europe with its northern range limit in southern Fennoscandia (Croose et al. 2018). In most countries, polecat populations are suspected to be declining, although the reasons for this decline are poorly understood and data are lacking in many countries (Blandford 1987, Croose et al. 2018). Habitat selection of polecats at the 3rd order is relatively well studied, showing that they select for diverse habitats including marshes, woodland and meadows, while dense urban areas are avoided (Lodé 1994, Baghli et al. 2005, Zabala et al. 2005). They avoid snow and cold weather, seeking shelter in farmhouses and villages during winter months (Weber 1989a, Jedrzejewski et al. 1993). This is likely because these influence polecat survival. Polecats are prone to quickly lose heat due to their long and thin bodies (Iversen 1972, Korhonen et al. 1983, Meshcherskii et al. 2003). Furthermore, snow influences their ability to capture prey, as most prey species hide under the snow while the polecat is too small to dig through the snow and too large to hunt below the snow (Weber 1987, 1989b, Jedrzejewski et al. 1993). We would thus expect snow cover to be an important factor limiting the distribution of the polecat, but it is still

uncertain if the effects of climate and snow on individuals translate to effects at the distribution level.

In Sweden up until 1950, polecats where only reported to be found in the southernmost part of the country (Götaland in Fig. 1). However, after 1950, there has been an increase in sightings of polecats further north (Udvardy and Siivonen 1968; in Svealand in Fig. 1). Climate models from the Swedish Meteorological and Hydrological Inst. (2021) showed that average temperatures in Sweden have increased over the period 1961–2021, while the number of days with snow on the ground have decreased. This suggests that climate limits the distribution of the polecat in Sweden. However, the relative importance of climate and habitat in determining the distribution of the polecat in Sweden are unknown.

In this study, we investigated the relative importance of habitat characteristics and climate in determining the habitat suitability for polecats in Sweden at a national scale. We hypothesized that 1) climate, and specifically the number of snow days, was the most important factor limiting polecat distribution, and 2) that, as the number of snow days decreases, habitat suitability increases in northern Sweden. To test these hypotheses, we used sightings data in combination with national maps of geomorphology, climate, land-cover and human pressure to predict current and future habitat suitability for polecats in Sweden using Maxent models. Finally, we used climate predictions for the periods 2021–2050 and 2063–2098 to estimate the potential future distribution of polecats in Sweden.

Method

Study area

In this study, we focus on the distribution of polecats in Sweden (450.295 km^2). Biogeographically, geographically and climatically, Sweden can be divided into two parts, separated by the Limes Norrlandicus (Fig. 1; Berg et al. 1994). The landscape south of the Limes Norrlandicus is characterized by the presence of some hardwood forest and a larger proportion of deciduous trees while the landscape north of this line mostly lacks hardwood trees and is dominated by coniferous forest. North of the line, most forests are used for forestry and agriculture is patchy and mostly present in the river valleys and around the coast all the way up north to the Finnish border (Angelstam et al. 2020). In Norrland, altitude increases from east to west. Snow depth north of Limes Norrlandicus is often above 30 cm while south of the line it rarely passes fifteen centimetres of snow (Swedish Meteorological and Hydrological Inst. 2021). Human population density is high in the southern regions and along the coasts, while for most of northern Sweden, population density is low.

Polecat sightings data

To determine the distribution and habitat suitability of polecats in Sweden, we used sightings data of polecats
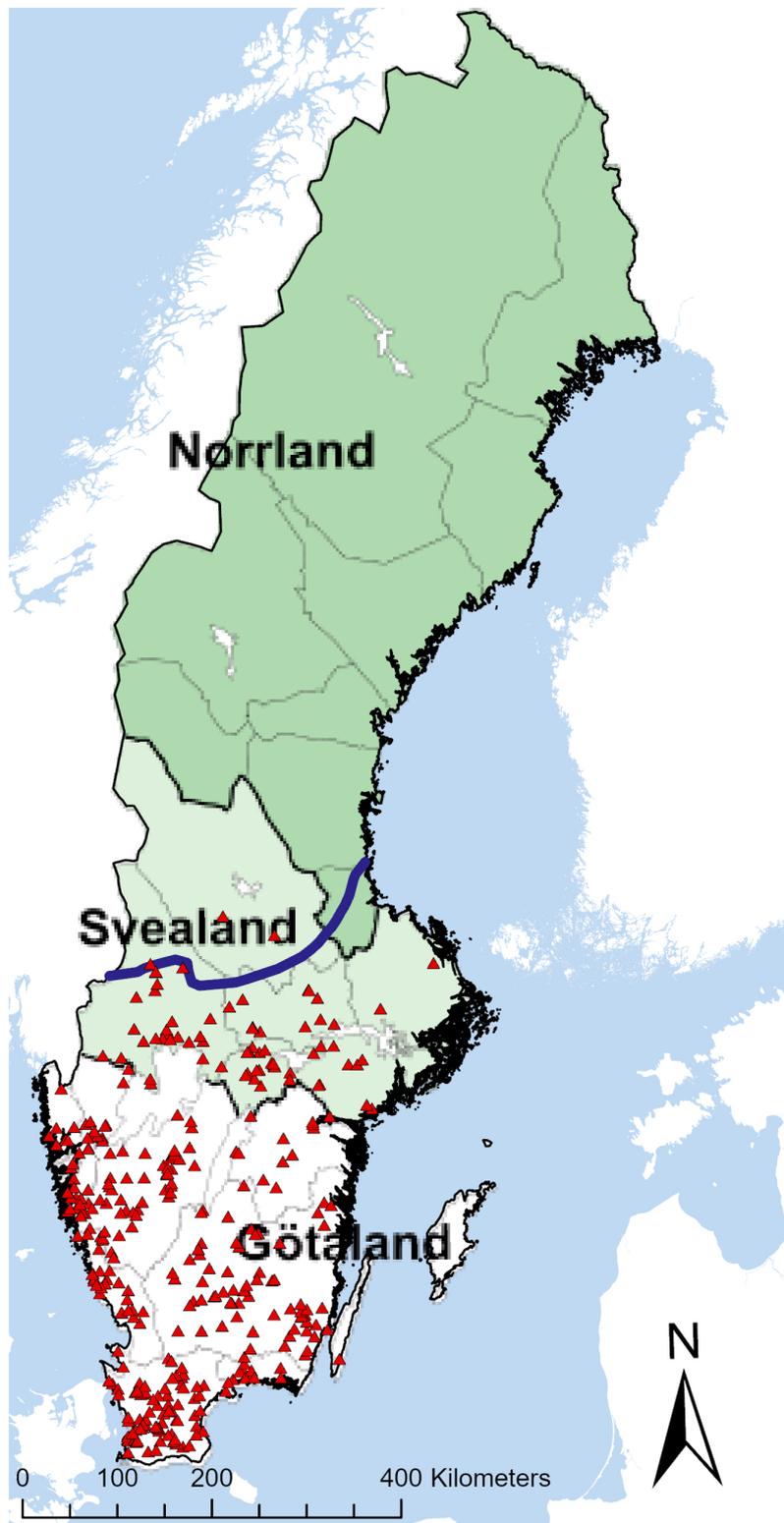
Figure 1. Map of Sweden showing the distinction of Sweden into three regions (Götaland, Svealand and Norrland) as well as the used polecat sightings (red triangles) and the geographical line crossing Svealand and the bottom of Norrland (Limes Norrlandicus; in blue).

gathered by volunteers and documented to the Swedish Species Information Centre between 1960 and 2020 (Fig. 1; Swedish Species Information Centre 2020). We validated data at the edge of the distribution by contacting the person that reported the sighting, and removed data points if there was uncertainty about the sighting, we also removed data which was categorized as roadkill. As a result we discarded 44 of the 425 sightings before analysis. Due to an increase of popularity of the sightings platform, the majority of sightings (78%) used in the analyses was from the period 2010–2020.

Covariate selection

We used nine covariates distributed over four different categories to test our hypotheses (Table 1). We included these covariates based on habitat and diet preferences of the polecat found in previous studies (see Supporting information for a more complete description of the covariates and why we included these; Blandford 1987, Costa et al. 2014, Skumatov et al. 2016, Croose et al. 2018). All parameters were rasterized and aggregated to 1-km² grid cells over the whole of Sweden in ArcGis Pro ver. 2.6.0 (Supporting information; Esri 2021). Due to incomplete data in some covariates, we only included grid cells that had complete data for all covariates. This meant that we discarded sightings data (n = 21) from grid cells with missing covariate data, resulting in 360 locations of polecat presence that we used in our analyses.

Habitat suitability model

Data selection
We used the software MaxEnt 3.4.3 (Phillips et al. 2004) for building the habitat suitability model, by calling MaxEnt from R (ver. 4.0.5; www.r-project.org/) using the packages raster (ver. 3.4-10; Hijmans et al. 2020) and kuenm (ver. 1.1.6; Cobos et al. 2019). We thinned the sightings only selecting one sighting per 1-km² grid cell. We then randomly selected 20% of the sightings data for validation (n = 75). We then split the remaining data into training (80%, n = 237) and testing data (20%, n = 60). Furthermore, we sampled 10 000 random background points over the whole of Sweden, ensuring that each random point had a unique combination of environmental values.

Bias correction for sampling intensity
Due to the nature of citizen science data it is prone to come with a bias. This bias manifests itself mostly in a discrepancy in spatial sampling effort (Tang et al. 2021). To account for this bias, we created a density kernel (as recommended by Kramer-Schadt et al. 2013) based on all mustelid sightings (n = 25 686) reported to the Swedish Species Information Centre between 1972 and 2021 (Swedish Species Information Centre 2020), except for the Eurasian badger *Meles meles*, the wolverine *Gulo gulo* and the polecat. We excluded the badger and wolverine as we expect this species to be much easier to identify and see compared to the polecat and other mustelids. Furthermore, badger and wolverine have a limited distribution in Sweden, while all other species – Eurasian otter *Lutra lutra*, pine marten *Martes martes*, American mink *Neovison vison*, stoat *Mustela erminea* and weasel *Mustela nivalis* – have a distribution that covers the whole of Sweden (Swedish Species Information Centre 2020). We created the kernel using the 'Kernel Density' function in ArcGIS Pro (Esri 2021) including both the mustelid sighting coordinates and the 1 km² raster grid used for the covariates. The use of this density kernel is based on the assumption that people reporting other mustelids would also report a polecat if they saw one, and thus that the distribution of mustelid sightings is representative of the distribution of potential polecat reporters.

Model selection
We used algorithms in the kuenm package (kuenm_varcomb, kuenm_cal and kuen_ceval) to optimize the covariates and inputs for features and regularization parameters. To account for multi-collinearity, we performed a spearman correlation analysis on all covariates. If covariates where strongly correlated (r > 0.75) we selected one based on biological relevance. This resulted in the omission of minimum temperature as it was strongly correlated with the number of snow days (r = 0.83). We used the density kernel of mustelid sightings as a bias file in all analyses (Supporting information). We used the kuenm package to test the fit of all possible combinations of covariates, where we limited the amount of covariates to a minimum of four for computational reasons. To decide which set of covariates to use in the final model, we ran all models with different combinations of regularization modifiers (0.1, 0.25, 0.5, 1, 2) and features (Linear, Quadratic and Product). This resulted in 163 unique sets of covariates and a total of 2445 models. Each of these models was sequentially run on the training data, after which the test data was used to determine the test omission rate. We selected the best model based on the following criteria: A p-value below 0.05 based on Partial ROC (Peterson et al. 2008), a test omission rate lower than 0.05 and the lowest Akaike's information criteria (AIC) value (Cavanaugh and Neath 2011). We ran all models for a maximum of 500 iterations with a convergence threshold of 10^{-5}.

Model results and significance testing
We then ran ten bootstrapped runs of the highest-ranking model and present the median and standard deviations based on the ten bootstrapped runs for result interpretation. Model output includes both a continuous cloglog output giving an index of relative suitability over the extent of the study area, and a binary representation of the Maxent output as areas of suitability based on a 10% training omission rate threshold. The 10% training omission rate threshold is the lowest cloglog value when allowing for 10% omission rate (Muscarella et al. 2014). As we were primarily interested in the potentially suitable habitat for polecats in Sweden, we decided to only interpret the binary output. To estimate the importance of each covariate in determining habitat

Table 1. Description, Resolution, time period, file type and source of all covariates included in the analysis separated into four categories.

Climate	Description	Resolution	Time period	Original file type	Source
Minimum winter temperature	Minimum temperature in the months December, January, February	1 km^2	1970–2000	.TIF	WorldClim: www.worldclim.org/data/worldclim21.html
Number of snow days	The number of days were snow depth was more than 20 mm	Average per municipality	1961–2098	.SHP	SMHI: www.smhi.se/en/weather/observations/snow-depth/
Human pressure					
Human footprint	Index for relative human footprint based on population density, land-use and infrastructure	1 km^2	1995–2004	.TIF	SEDAC: https://sedac.ciesin.columbia.edu/data/set/wildareas-v3-2009-human-footprint
Land cover					
Deciduous forest	Proportion deciduous forest	10 m^2	2017–2019	.TIF	Naturvardsverket: www.naturvardsverket.se/verktyg-och-tjanster/kartor-och-karttjanster/nationella-marktackedata/
Coniferous forest	Proportion coniferous forest	10 m^2	2017–2019	.TIF	
Open landscape	Proportion open landscape	10 m^2	2017–2019	.TIF	
Water availability	Percentage area within 30 m from water	10 m^2	2017–2019	.TIF	Copernicus land: https://land.copernicus.eu/pan-european/high-resolution-layers/water-wetness/status-maps/water-wetness-2018
Geomorphology					
Elevation (DEM)	Height above sea-level	25 m^2	2013	.TIF	https://land.copernicus.eu/imagery-in-situ/eu-dem/eu-dem-v1.1
Soil moisture	Index of soil moisture from dry to wet	10 m^2	2006–2012	.TIF	https://metadatakatalogen.naturvardsverket.se/metadatakatalogen/GetMetaDataById?id=cae71f45-b463-447f-804f-28478969b19b0

suitability, we estimated the percent contribution and permutation importance of each covariate and performed a jack-knife test. To validate our model we calculated the omission rate based on our validation data.

We also ran the models on a smaller extent only covering the part of Sweden where we have sightings data. We did this to test if including a large area without sightings data (the majority of northern Sweden) could lead to spurious correlations with habitat covariates. In this extra analysis, we reduced the extent of the study region by excluding all habitat north of the most northward sighting and resized all parameters.

Model projection

To test our second hypothesis, we projected the highest-ranking model with future climate predictions of the amount of snow days in Sweden. For this, we used two projection periods based on the 4.5 Representatitive Concentration Pathway (RCP) scenario (Thomson et al. 2011): 2021–2050 and 2063–2098 (Swedish Meteorological and Hydrological Inst. 2021). All other settings and covariates were kept the same. We allowed the predictions to extrapolate from the current values for snow days as the predicted number of snow days ranged outside of the current values. We used two different extrapolation options: extrapolate and extrapolate with clamping, and selected between these based on the response curves. We evaluated projection performance using mobility-oriented parity (Owens et al. 2013).

Results

Model settings and performance

The top-ranking model included six covariates with an average AUC of 0.908 and an omission rate of 0.042 (Table 2; Supporting information). The number of snow days was the most important covariate determining habitat suitability of polecats in Sweden with a permutation importance of 71.5%. Polecat habitat suitability decreased with the number of snow days, where areas with > 180 snow days had an estimated suitability of zero (Fig. 2a). Polecat habitat suitability further decreased with the proportion of coniferous forest (Fig. 2b), and increased with human footprint index (Fig. 2c). Habitat suitability showed an optimum at a proportion of open landscape of 0.35 (Fig. 2d). We did not interpret

Table 2. Covariates and their percentage of contribution to the variation of the model with permutation importance per covariate as validation of the contribution percentage.

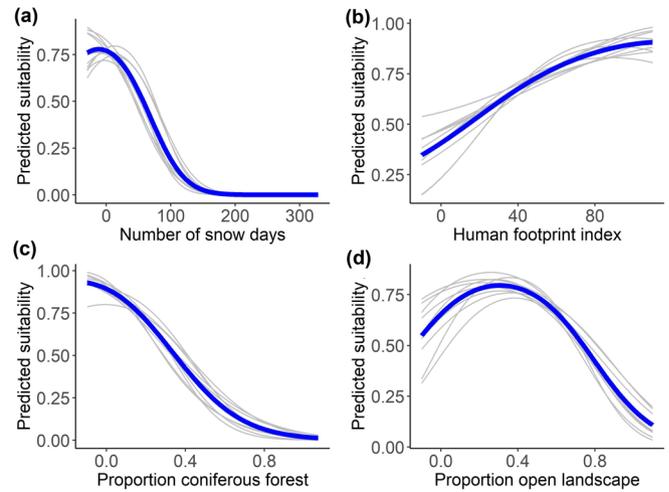| Variable	Percent contribution	Permutation importance
Number of snow days	52.0	71.5
Coniferous forest	17.7	16.5
Human footprint index	7.8	5.6
Open landscape	5.4	4.2
Water availability	15.6	1.2
Soil moisture index	1.5	0.9

Figure 2. The response of polecat habitat suitability to (a) the number of snow days, (b) the proportion of coniferous forest, (c) the human footprint index and (d) the proportion open landscape. The blue line shows the mean of ten bootstrapped runs, the grey lines the individual runs.

the response curves of proportion water availability and soil moisture index as they contributed very little to the model and had large standard deviations (Supporting information). The jackknife analysis showed that even though the contribution of human footprint is not very high, human footprint explains a large percentage of the model outcome, second to number of snow days (Supporting information). The number of snow days was also the variable that decreased the training gain the most when removed and thus held the most information that is not present in the other variables (Supporting information). The response curves of the model that included only southern Sweden showed no clear difference from those including the entire country (Supporting information).

Current and projected habitat suitability for the polecat in Sweden

Based on the highest-ranking model, we estimated that currently 62.3% of the total area south of the Limes Norrlandicus is suitable habitat for polecats while only 0.6% of the area north of the Limes Norrlandicus is estimated to be suitable (Fig. 3a). When predicting the suitability for the projected days with snow cover for the period 2021–2053 we found a slight increase with 69.4% of the area south, and 1.9% of the habitat north of the Limes Norrlandicus estimated to be suitable (Fig. 3b). The prediction for the projected snow cover for the period 2063–2098 showed no further suitability increase south of Limes Norrlandicus (69.1%), but a significant increase to 9.4% north of the Limes Norrlandicus (Fig. 3c). Most of this increase in habitat suitability is around the east coast. The mobility-oriented parity analysis showed location specific variation in transferability for the two predictions (Supporting information), while there was a negligible difference between the projection options extrapolation or extrapolation with clamping (Supporting information).
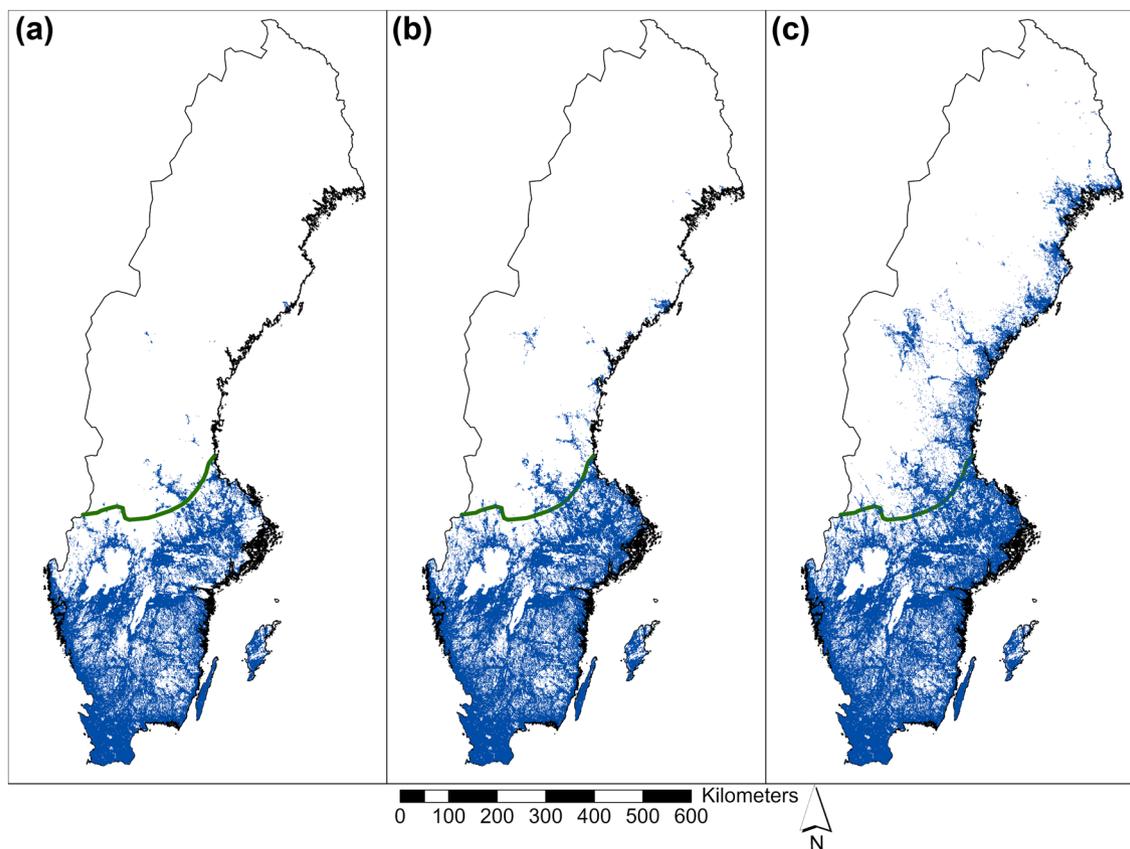
Figure 3. Estimated habitat suitability for polecat in Sweden at a 1-km² resolution using a 10% omission rate threshold for (a) the current situation (1991–2013), (b) the period 2021–2050 and (c) the period 2069–2098. Suitable habitat is shown in blue, the green line indicates the Limes Norrlandicus.

Discussion

We used sightings data and national maps of environmental and climatic variables to test if the polecat distribution at the northern part of its range is limited by climate or land use. Our models predicted high habitat suitability for polecats within the known distribution range in Sweden. Generally, we find a good congruence between the locations with sightings data and the predicted suitability in our model. The main exception being the region in the northeast of the distribution, just south of the Limes Norrlandicus (Uppland; Fig. 1, 3a), where we estimated high suitability (Fig. 3a) but where very few sightings have been reported (Fig. 1). There are some indications, based on experiences from trappers, that polecats have recently moved into this area (Thurfjell and Tomasson 2017). This is further supported by some isolated sightings in the Swedish Species Information Centre from the past 5 years (Swedish Species Information Centre 2020). Based on these external indications and the low omission rate we conclude that the model predicted the current situation well.

The number of snow days was the most important factor determining the habitat suitability of polecats in Sweden, confirming our hypothesis that climate limits the species' distribution. Furthermore, we found that habitat suitability was

highest in areas with a low proportion of coniferous forest, an intermediate level of open habitat, and with a high human footprint index. To our knowledge, previous studies on habitat suitability at national scales for polecats are lacking. However, our results are in line with what would be expected based on previous studies at smaller spatial scales, showing that polecats select for diverse habitats and avoid coniferous forest (Baghli and Verhagen 2005, Zabala et al. 2005). The exact mechanisms through which snow limits polecats are poorly understood and need further investigation. However, we expect that it is a combination of the cost of thermoregulation, which is relatively high due to their small, long and thin body shape (Iversen 1972, Korhonen et al. 1983, Meshcherskii et al. 2003), as well as limited hunting capacity, as they are too large to hunt under the snow like weasels and stoats (Aunapuu and Oksanen 2003). This might also explain why polecats heavily rely on human settlements as resting sites during winter (Weber 1989a, b, Jedrzejewski et al. 1993). Further studies into the habitat suitability for polecats in other parts of its range would be very valuable to further test how habitat selection studies at small spatial scales translate to habitat suitability at national and continental scales.

In accordance with our second hypothesis, we found that the habitat suitability for polecats in Sweden will likely

increase in the coming decades as climate projections show a decrease in number of snow days (Swedish Meteorological and Hydrological Inst. 2021). This increase is most likely to happen along the coast of the Baltic Sea where the landscape is more diverse. Consequently, habitat will become the limiting factor determining the polecat distribution as large expanses of coniferous forest still reduce the proportion of suitable habitat in Norrland to a predicted 9.4% in 2098 (Fig. 3). We would expect a similar increase in other countries at the northern and eastern edge of the distribution such as Norway, Finland and Russia, mainly along river valleys and other more diverse landscapes. Furthermore, it indicates that polecat populations might increase in locations where altitudinal differences in snow cover currently limit the species. This might result in an increase in polecat populations in these areas, in contrast to the decline in many other parts of its range (Croose et al. 2018).

One of the caveats of our study is that our analysis was done using citizen science data. While citizen science is becoming a more common source of data especially for habitat suitability studies, there are certain drawbacks (Brossard et al. 2005, Aceves-Bueno et al. 2017). The data are less precise and are prone to both spatial and temporal biases (Dickinson et al. 2010). These biases could have led to over-representation of polecats in human dominated areas skewing the model (Mair et al. 2017). However, the density kernel based on reported mustelid sightings should have corrected for this spatial bias. Furthermore, given our interpretation at a national scale of only the maps based on the 10% training omission rate threshold, we do not think that spatial and temporal biases have severely impacted our conclusions. Especially, as polecats are present in human dominated areas all over its distribution range (Weber 1995, Baghli et al. 2005, Sainsbury et al. 2020). Nevertheless, we would encourage further investigation based on e.g. genetic or camera trap data to further elucidate the response of polecats to human dominated landscapes at both spatial and temporal scales.

To conclude, our study suggests that climate, and not habitat, is limiting the current polecat distribution in Sweden, and that consequently, we would expect a range expansion in the near future. Furthermore, we are the first to show that habitat suitability of polecats at a national scale aligns with habitat selection at smaller spatial scales, showing that polecats select for diverse habitats, including human-altered landscapes. However, the exact mechanisms through which snow limits polecats are still poorly understood. Climate change is happening globally, and thus we expect our results to be applicable to other parts of the polecat range as well as other species showing similar limits in their distribution, e.g. the European hare (*Lepus europaeus*; Thulin 2003, Hacklander and Schai-Braun 2019). This might result in changes in the composition of wildlife communities, changing interspecific interactions and potentially resulting in trophic cascades (Elmhagen et al. 2015). In order to better predict and map these changes, we encourage similar studies on polecats and other species, both in Sweden and in other locations at the edge of their range.

Author contributions

Transparent peer review

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi:10.5061/dryad.j0zpc86hn (Osinga et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Aceves-Bueno, E., Adeleye, A. S., Feraud, M., Huang, Y., Tao, M., Yang, Y. and Anderson, S. E. 2017. The accuracy of citizen science data: a quantitative review. – Bull. Ecol. Soc. Am. 98: 278–290.

Angelstam, P., Manton, M., Green, M., Jonsson, B., Mikusiński, G., Svensson, J. and Maria Sabatini, F. 2020. Sweden does not meet agreed national and international forest biodiversity targets: a call for adaptive landscape planning. – Landsc. Urban Plan. 202: 103–838.

Aunapuu, M. and Oksanen, T. 2003. Habitat selection of coexisting competitors: a study of small mustelids in northern Norway. – Evol. Ecol. 17: 371–392.

Baghli, A. and Verhagen, R. 2005. Activity patterns and use of resting sites by polecats in an endangered population. – mamm 69: 211–222.

Baghli, A., Walzberg, C. and Verhagen, R. 2005. Habitat use by the European polecat *Mustela putorius* at low density in a fragmented landscape. – Wildl. Biol. 11: 331–339.

Balestrieri, A., Bogliani, G., Boano, G., Ruiz-González, A., Saino, N., Costa, S. and Milanesi, P. 2016. Modelling the distribution of forest-dependent species in human-dominated landscapes:

patterns for the pine marten in intensively cultivated lowlands. – PLoS One 11: e0158203.

Blandford, P. R. S. 1987. Biology of the polecat *Mustela putorius*: a literature review. – Mammal Rev. 17: 155–198.

Brossard, D., Lewenstein, B. and Bonney, R. 2005. Scientific knowledge and attitude change: the impact of a citizen science project. – Int. J. Sci. Educ. 27: 1099–1121.

Cavanaugh, J. E. and Neath, A. A. 2011. Akaike's information criterion: background, derivation, properties and refinements. – In: Lovric, M. (ed.), International encyclopedia of statistical science. Springer, pp. 26–29.

Cobos, M. E., Peterson, A. T., Barve, N. and Osorio-Olvera, L. 2019. kuenm: an R package for detailed development of ecological niche models using Maxent. – PeerJ 7: e6281.

Costa, M., Fernandes, C. and Santos-Reis, M. 2014. Ecology and conservation of the polecat *Mustela putorius* (Linnaeus, 1758) in Portugal: a review. – Munibe Monogr. Nat. Ser. 3: 79–87.

Croose, E., Duckworth, J. W., Ruette, S., Skumatov, D. V., Kolesnikov, V. V. and Saveljev, A. P. 2018. A review of the status of the western polecat *Mustela putorius*: a neglected and declining species? – Mammalia 82: 550–564.

Dickinson, J. L., Zuckerberg, B. and Bonter, D. N. 2010. Citizen science as an ecological research tool: challenges and benefits. – Annu. Rev. Ecol. Evol. Syst. 41: 149–172.

Elith, J. and Leathwick, J. R. 2009. Species distribution models: ecological explanation and prediction across space and time. – Annu. Rev. Ecol. Evol. Syst. 40: 677–697.

Elmhagen, B., Kindberg, J., Hellström, P. and Angerbjörn, A. 2015. A boreal invasion in response to climate change? Range shifts and community effects in the borderland between forest and tundra. – Ambio 44: S39–S50.

Esri 2021. 2D, 3D and 4D GIS Mapping Software | ArcGIS Pro. – www.esri.com/en-us/arcgis/products/arcgis-pro/overview.

Guisan, A. and Zimmermann, N. E. 2000. Predictive habitat distribution models in ecology. – Ecol. Model. 135: 147–186.

Guralnick, R. 2007. Differential effects of past climate warming on mountain and flatland species distributions: a multispecies North American mammal assessment. – Global Ecol. Biogeogr. 16: 14–23.

Hacklander, K. and Schai-Braun, S. 2019. Lepus europaeus. – The IUCN Red List of Threatened Species 2019: e. T41280A45187424, http://dx.doi.org/10.2305/IUCN. UK.2019-1.RLTS.T41280A45187424.en.

Hampe, A. 2011. Plants on the move: the role of seed dispersal and initial population establishment for climate-driven range expansions. – Acta Oecol. 37: 666–673.

Hijmans, R. J., van Etten, J., Sumner, M., Cheng, J., Baston, D., Bevan, A., Bivand, R., Busetto, L., Canty, M., Fasoli, B., Forrest, D., Ghosh, A., Golicher, D., Gray, J., Greenberg, J. A., Hiemstra, P., Hingee, K., Ilich, A., Karney, C., Mattiuzzi, M., Mosher, S., Naimi, B., Nowosad, J., Pebesma, E., Lamigueiro, O. P., Racine, E. B., Rowlingson, B., Shortridge, A., Venables, B. and Wueest, R. 2020. raster: geographic data analysis and modelling. – https://cran.r-project.org/web/packages/raster/ index.html.

Hirzel, A. H., Le Lay, G., Helfer, V., Randin, C. and Guisan, A. 2006. Evaluating the ability of habitat suitability models to predict species presences. – Ecol. Model. 199: 142–152.

Iversen, J. A. 1972. Basal energy metabolism of mustelids. – J. Comp. Physiol. 81: 341–344.

Jedrzejewski, W., Jędrzejewska, B. and Brzeziński, M. 1993. Winter habitat selection and feeding habits of polecats *Mustela putorius*

in the Białowieża National Park, Poland. – Z. Säugetierkd. 58: 75–83.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. – Ecology 61: 65–71.

Korhonen, H., Harri, M. and Asikainen, J. 1983. Thermoregulation of polecat and raccoon dog: a comparative study with stoat, mink and blue fox. – Comp. Biochem. Physiol. A Comp. Physiol. 74: 225–230.

Kramer-Schadt, S., Niedballa, J., Pilgrim, J. D., Schröder, B., Lindenborn, J., Reinfelder, V., Stillfried, M., Heckmann, I., Scharf, A. K., Augeri, D. M., Cheyne, S. M., Hearn, A. J., Ross, J., Macdonald, D. W., Mathai, J., Eaton, J., Marshall, A. J., Semiadi, G., Rustam, R., Bernard, H., Alfred, R., Samejima, H., Duckworth, J. W., Breitenmoser-Wuersten, C., Belant, J. L., Hofer, H. and Wilting, A. 2013. The importance of correcting for sampling bias in MaxEnt species distribution models. – Divers. Distrib. 19: 1366–1379.

Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B. and Ackerly, D. D. 2009. The velocity of climate change. – Nature 462: 1052–1055.

Lodé, T. 1994. Environmental factors influencing habitat exploitation by the polecat *Mustela putorius* in western France. – J. Zool. 234: 75–88.

Lundy, M., Montgomery, I. and Russ, J. 2010. Climate change-linked range expansion of Nathusius' pipistrelle bat, *Pipistrellus nathusii* (Keyserling & Blasius, 1839). – J. Biogeogr. 37: 2232–2242.

Mair, L., Harrison, P. J., Jönsson, M., Löbel, S., Nordén, J., Siitonen, J., Lämås, T., Lundström, A. and Snäll, T. 2017. Evaluating citizen science data for forecasting species responses to national forest management. – Ecol. Evol. 7: 368–378.

Mccain, C. M. and King, S. R. B. 2014. Body size and activity times mediate mammalian responses to climate change. – Global Change Biol. 20: 1760–1769.

Meshcherskii, I. G., Rozhnov, V. V. and Naidenko, S. V. 2003. On certain properties of water and energy metabolism in representatives of *Martes* and *Mustela* genera (Mammalia: Mustelidae). – Biol. Bull. 30: 406–410.

Moreno-Amat, E., Mateo, R. G., Nieto-Lugilde, D., Morueta-Holme, N., Svenning, J. and García-Amorena, I. 2015. Impact of model complexity on cross-temporal transferability in Maxent species distribution models: an assessment using paleobotanical data. – Ecol. Model. 312: 308–317.

Muscarella, R., Galante, P. J., Soley-Guardia, M., Boria, R. A., Kass, J. M., Uriarte, M. and Anderson, R. P. 2014. ENMeval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. – Methods Ecol. Evol. 5: 1198–1205.

Osinga, T., Thurfjell, H. and Hofmeester, T. R. 2022. Data from: Snow limits polecat *Mustela putorius* distribution in Sweden. – Dryad Digital Repository, https://doi:10.5061/dryad. j0zpc86hn.

Owens, H. L., Campbell, L. P., Dornak, L. L., Saupe, E. E., Barve, N., Soberón, J., Ingenloff, K., Lira-Noriega, A., Hensz, C. M., Myers, C. E. and Peterson, A. T. 2013. Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. – Ecol. Model. 263: 10–18.

Pacifici, M., Rondinini, C., Rhodes, J. R., Burbidge, A. A., Cristiano, A., Watson, J. E. M., Woinarski, J. C. Z. and Di Marco, M. 2020. Global correlates of range contractions and expansions in terrestrial mammals. – Nat. Commun. 11: 2840.

Peterson, A. T., Papeş, M. and Soberón, J. 2008. Rethinking receiver operating characteristic analysis applications in ecological niche modeling. – Ecol. Model. 213: 63–72.

Phillips, S. J., Dudik, M. and Schapire, R. E. 2004. Maxent software for species distribution modeling. – https://biodiversityinformatics.amnh.org/open_source/maxent/.

Phillips, S. J., Anderson, R. P. and Schapire, R. E. 2006. Maximum entropy modeling of species geographic distributions. – Ecol. Model. 190: 231–259.

Robinet, C. and Roques, A. 2010. Direct impacts of recent climate warming on insect populations. – Integr. Zool. 5: 132–142.

Sainsbury, K. A., Shore, R. F., Schofield, H., Croose, E., Hantke, G., Kitchener, A. C. and McDonald, R. A. 2020. Diets of European polecat *Mustela putorius* in Great Britain during fifty years of population recovery. – Mammal Res. 65: 181–190.

Skumatov, D., Abramov, A. V., Herrero, J., Kitchener, A., Maran, T., Kranz, A., Sándor, A., Saveljev, A., Savouré-Soubelet, A., Guinot-Ghestem, M., Zuberogoitia, I., Birks, J. D. S., Weber, A., Melisch, R. and Ruette S. 2016. *Mustela putorius*. – IUCN Red List Threat. Species 2016: e.T41658A45214384, https://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T41658A45214384.en.

Swedish Meteorological and Hydrological Inst. 2021. Snow depth of Sweden. – www.smhi.se/en/weather/sweden-weather/snow-depth/.

Swedish Species Information Centre 2020. Species observation system – Artportalen. – www.artportalen.se/.

Tang, B., Clark, J. S. and Gelfand, A. E. 2021. Modeling spatially biased citizen science effort through the eBird database. – Environ. Ecol. Stat. 28: 609–630.

Thomas, C. D. and Lennon, J. J. 1999. Birds extend their ranges northwards. – Nature 399: 213–213.

Thomson, A. M., Calvin, K. V., Smith, S. J., Kyle, G. P., Volke, A., Patel, P., Delgado-Arias, S., Bond-Lamberty, B., Wise, M. A., Clarke, L. E. and Edmonds, J. A. 2011. RCP4.5: a pathway for stabilization of radiative forcing by 2100. – Clim. Change 109: 77.

Thulin, C. G. 2003. The distribution of mountain hares *Lepus timidus* in Europe: a challenge from brown hares *L. europaeus*? – Mammal Rev. 33: 29–42.

Thurfjell, H. and Tomasson, L. 2017. Biogeografisk uppföljning Iller <SLU ID: SLU.2017.5.2-40>: 3.

Troia, M. J., Kaz, A. L., Niemeyer, J. C. and Giam, X. 2019. Species traits and reduced habitat suitability limit efficacy of climate change refugia in streams. – Nat. Ecol. Evol. 3: 1321–1330.

Udvardy, M. D. F. and Siivonen, L. 1968. Pohjolan Nisäkkäät (Mammals of northern Europe). – J. Mammal. 49: 167–168.

Weber, D. 1987. Zur Biologie des Iltisses (*Mustela putorius* L.) und den Ursachen seines Rückganges in der Schweiz. – PhD thesis, Univ. of Basel, Switzerland.

Weber, D. 1989a. Foraging in polecats (*Mustela putorius* L.) of Switzerland: the case of a specialist anuran predator. – Z. Säugetierkd. 54: 377–392.

Weber, D. 1989b. The ecological significance of resting sites and the seasonal habitat change in polecats (*Mustela putorius*). – J. Zool. 217: 629–638.

Weber, D. 1995. *Mustela putorius*. – Säugetiere Schweiz 8235: 389–394.

Zabala, J., Zuberogoitia, I. and Martínez-Climent, J. A. 2005. Site and landscape features ruling the habitat use and occupancy of the polecat (*Mustela putorius*) in a low density area: a multiscale approach. – Eur. J. Wildl. Res. 51: 157–162.

Zielinski, W. J., Dunk, J. R., Yaeger, J. S. and LaPlante, D. W. 2010. Developing and testing a landscape-scale habitat suitability model for fisher (*Martes pennanti*) in forests of interior northern California. – For. Ecol. Manage. 260: 1579–1591.