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Research article

Wolverine density distribution reflects past persecution and current management in Scandinavia

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After centuries of intense persecution, several large carnivore species in Europe and North America have experienced a rebound. Today's spatial configuration of large carnivore populations has likely arisen from the interplay between their ecological traits and current environmental conditions, but also from their history of persecution and protection. Yet, due to the challenge of studying population-level phenomena, we are rarely able to disentangle and quantify the influence of past and present factors driving the distribution and density of these controversial species. Using spatial capture-recapture models and a data set of 742 genetically identified wolverines *Gulo gulo* collected over ½ million km² across their entire range in Norway and Sweden, we identify landscape-level factors explaining the current population density of wolverines in the Scandinavian Peninsula. Distance from the relict range along the Swedish–Norwegian border, where the wolverine population survived a long history of persecution, remains a key determinant of wolverine density today. However, regional differences in management and environmental conditions also played an important role in shaping spatial patterns in present-day wolverine density. Specifically, we found evidence of slower recolonization in areas that had set lower wolverine population goals in terms of the desired number of annual reproductions. Management of transboundary large carnivore populations at biologically relevant scales may be inhibited by administrative fragmentation. Yet, as our study shows, population-level monitoring is an achievable prerequisite for a comprehensive understanding of the distribution and density of large carnivores across an increasingly anthropogenic landscape.

Keywords: abundance, density, distribution, *Gulo gulo*, large carnivores, noninvasive monitoring, spatial capture-recapture, transboundary wildlife

Introduction

Species distributions we observe today are the result of not only ecological traits and current local environmental conditions, but also land-use history, human activity, and management strategies (Donohue et al. 2000, Foster et al. 2003, Di Marco



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and Santini 2015). Emerging disturbance regimes, such as altered frequency and intensity of extreme weather and climate events (Ummenhofer and Meehl 2017), further impact species distributions. Identifying and disentangling the factors that lead to the distribution and dynamics of species is one of the most profound and long-standing research areas in ecology, with both fundamental and applied implications (Guisan and Zimmermann 2000, Elith and Leathwick 2009, Jetz et al. 2019).

Humans are the main transformers of Earth's ecosystems (Ellis 2011, Pereira et al. 2012, Waters et al. 2016), with a growing list of documented effects on wildlife (Yackulic et al. 2011, Tucker et al. 2018). Despite a broad overall consistency in wildlife responses to anthropogenic disturbances, there is considerable variability in scale, magnitude, and pattern of human impacts (Tablado and Jenni 2017, Gaynor et al. 2018, Tucker et al. 2018). A popular example is the case of large carnivore species that have undergone substantial range contractions due to intensive persecution by humans. While many species continue to struggle, some have in recent decades successfully recolonized part of their historic range, particularly in Western Europe and North America (Linnell et al. 2001, Zedrosser et al. 2011, Chapron et al. 2014, Ripple et al. 2014, Ingeman et al. 2022). Limited understanding of factors shaping the spatial configuration of carnivore populations poses a challenge to science and management, and the current knowledge gaps may hinder predictions of future responses in the face of increasing human pressure.

The fall and rise of wolverines *Gulo gulo* in Scandinavia is a prime example of recovery of an iconic large carnivore following intense persecution and range contraction. The wolverine was historically distributed throughout most of the Scandinavian Peninsula (Landa et al. 2000, Flagstad et al. 2004). During the 19th and 20th centuries, intensive persecution of the wolverine reduced its range and population size drastically. By 1970, the population was functionally extinct in many areas with the exception of a narrow strip in the alpine region along the border between Sweden and Norway (Landa et al. 2000, Flagstad et al. 2004, Fig. 1). The situation was similarly grim in neighboring Finland, where wolverine observations were rare beyond the borderland with Russia (Lansink et al. 2020, Fig. 1). The wolverine finally received legal protection in both Norway and Sweden by 1973, later followed by Finland, and gradually recolonized many parts of its historical range in Fennoscandia (Flagstad et al. 2004, Aronsson and Persson 2017, Lansink et al. 2020). Today, the wolverine population is established across Norway and Sweden beyond the alpine refuge areas (Chapron et al. 2014, Gervasi et al. 2019, Bischof et al. 2020). The return of the wolverine has rekindled conflict with the sheep-farming industry and semidomesticated reindeer *Rangifer tarandus* husbandry (Flagstad et al. 2004, Hobbs et al. 2012, Persson et al. 2015, Aronsson and Persson 2017). The wolverine is listed on Appendix S2 of the Bern Convention for both countries and is therefore formally 'strictly protected'. However, because Norway is not a member of the European

Union, it is not bound by the same set of regulations. Wolverines are therefore subject to persistent lethal control in Norway, while they are strictly protected in Sweden under the European Union's Habitats Directive 92/43 (annex II, Habitats Directive 1992), and only recently were small hunting quotas (≈ 15) allowed for damage control purposes.

In a human-dominated world, understanding population-level drivers of species distribution, and particularly density, is important to understand and predict the potential for species–environment interactions in a management context. What we know about landscape and environmental factors influencing wolverine distribution and density has been cobbled together from a small patchwork of studies, often with limited spatial extent in various parts of the global distribution range of the species (Fisher et al. 2022). In Scandinavia, population and landscape-level determinants of wolverine distribution and density are poorly known. Historical (Landa et al. 2000) and current (Chapron et al. 2014) range maps suggest that recolonization in this anthropogenic landscape has been facilitated by favorable legislation and improved cultural acceptance (Linnell et al. 2001, Flagstad et al. 2004, Aronsson and Persson 2017). However, there is evidence that biophysical constraints, such as climate, habitat, and terrain, have played a greater role in shaping the current distribution of the wolverine at the continental scale (Cretois et al. 2021). Current management decisions use information that is largely based on data from the high-conflict alpine areas (Brøseth et al. 2010, Aronsson and Persson 2017), but would benefit from a better knowledge of the determinants of the wolverine's spatial variation in density across its entire Scandinavian range. Until recently, this was out of reach, because of the rarity and elusive behavior of the species, the vast geographic expanse of the population, and spatially incomplete surveys (Flagstad et al. 2004, Gervasi et al. 2016, Aronsson and Persson 2017).

Here, we set out to quantify the extent to which current wolverine population density across the Scandinavian Peninsula is affected by past and present conditions. Importantly, we do so for the entire $\frac{1}{2}$ million km² range of the species across Norway and Sweden. Three major challenges plague monitoring of elusive species, such as the wolverine, at ecologically relevant scales: 1) the collection of sufficiently detailed individual data from an entire population, 2) imperfect detection – i.e. not all individuals in the population are detected, and 3) a paucity of computationally efficient analytical tools to disentangle the effects of ecological drivers from both stochastic process noise and observation errors (Isaac et al. 2020, Cretois et al. 2021, van de Schoot et al. 2021). In this study, we tackled these challenges for the Scandinavian wolverine by analyzing a comprehensive capture-recapture data set of genetically identified wolverine individuals across the entire population in Norway and Sweden using recently developed efficient spatial capture-recapture (SCR) models (Bischof et al. 2020, Turek et al. 2021).

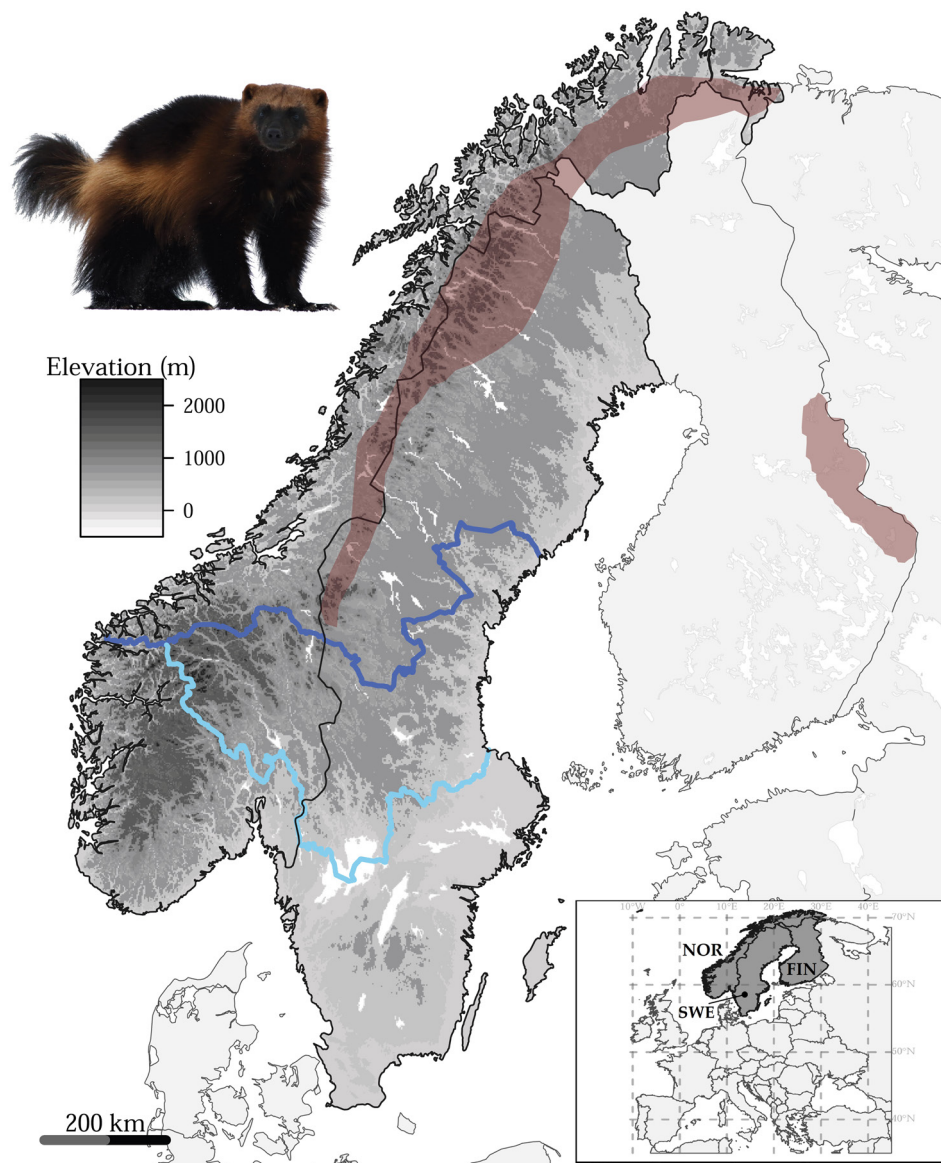


Figure 1. Approximate wolverine *Gulo gulo* distribution in the Scandinavian Peninsula (red polygon on the left) and Finland (red polygon on the right) in the 1970s, when the population range was at its lowest in modern times following intense human persecution (i.e. the relict range; Landa et al. 2000, Flagstad et al. 2004). Blue lines separate zones containing administrative units with shared population goals for the wolverine in Norway and Sweden (Table 1): above the dark blue line has the management goal of 10 or more annual wolverine reproductions, the zone above the light blue line allows less than 10 annual reproductions, and the zone below the light blue line has no management goal for the wolverine reproduction. We merged the zones below the dark blue line into one southern zone in each country. Photo credit: Karel Bartik/www.shutterstock.com.

Material and methods

Noninvasive genetic sampling

We used wolverine noninvasive genetic sampling (NGS) data from the Scandinavian large carnivore monitoring database (Rovbase ver. 3.0; www.rovbase.no and www.rovbase.se). This is one of the largest, long-term set of capture-recapture data of terrestrial wildlife globally (Smith et al. 2017, Tourani 2022). Wildlife authorities and volunteers conduct both structured searches and opportunistic sampling of putative

wolverine scats and hair on snow between December and June each year throughout the species' range in Norway and Sweden. The structured search tracks and locations of noninvasive samples are GPS recorded (Supporting information). Further details on wolverine NGS is provided elsewhere (Brøseth et al. 2010, Gervasi et al. 2016, Bischof et al. 2020). Samples were processed and analyzed by two dedicated DNA labs using a number of control measures to minimize genotyping errors, as described elsewhere (Ekblom et al. 2018, Flagstad et al. 2019, Lansink et al. 2022). First, samples were analyzed with a single nucleotide polymorphism-(SNP)-chip

with 96 markers; and, second, all individuals were analyzed with 19 microsatellite markers to determine species and identity of wolverine individuals, as well as their sex. We used NGS data collected between 1 December 2018 and 30 June 2019, which consisted of individual identity, sex, collection date, and coordinates associated with each wolverine sample. This sampling period represents the latest, most complete, semi-systematic wolverine NGS effort across the entire range of the wolverine population in Scandinavia to date (Flagstad et al. 2019, Bischof et al. 2020, Milleret et al. 2022). We minimized the probability of including juvenile (≤ 10 months old) individuals in the analysis by using only NGS data collected while tracking wolverine on snow, before emergence of cubs of the year from natal dens (Gervasi et al. 2016). Nonetheless, our data could still include subadult wolverines (< 2 years old) that may use space differently than adults. Subadult males, in particular, are more likely to initiate long-distance movements (Vangen et al. 2001), which may introduce an unknown and unmodeled source of individual heterogeneity in our study (Gimenez et al. 2018). We detected a few individuals ($n=3$ females and 21 males) that made long-distance movements of more than 40 km during the 2018/2019 monitoring season, and those detections (3 female and 29 male detections) – but not the individuals – were removed from the analysis, as they likely constitute dispersal events instead of movement within the home range.

Analysis

SCR models offer a flexible framework to account for imperfect detection of individuals and provide spatially explicit estimates of abundance (i.e. density) and other population parameters (Efford 2004, Borchers and Efford 2008, Royle et al. 2014). The SCR modeling framework can support flexible sampling configurations and incorporate both individual- and detector-level covariates to account for sources of heterogeneity in detectability, and spatial covariates to account for variation in density (Royle et al. 2014). Although building spatially indexed hierarchical models, such as SCR, can be computationally challenging or even prohibitive for large spatial extents, recent developments have resulted in dramatic improvements (Milleret et al. 2019, Turek et al. 2021, Zhang et al. 2023). Here, we build on these recent developments to study the landscape-scale determinants of the Scandinavian wolverine density.

Spatial capture-recapture model

We built a single-season (i.e. demographically closed) SCR model in a Bayesian framework by expanding on our previous work (Bischof et al. 2020). Our SCR model contained two hierarchical levels: 1) the observation submodel, accounting for imperfect and variable wolverine detectability during NGS, and 2) the ecological submodel, describing wolverine density as the main ecological process of interest in this study. Our SCR model estimated the following parameters: 1) the baseline detection probability p_0 ; detection probability at a trap or hypothetical detector located at an animal's activity

center s_i – a latent variable representing the expected location about which an individual uses space during the sampling period, 2) the spatial scale parameter of the detection function σ , 3) the number N of wolverine activity centers within the available habitat S (i.e. the detector grid and a buffer around it), which can be used to derive density D (below), and 4) the effects (regression coefficients β) of spatial and individual covariates on the detection probability and density.

The observation submodel

We used the conventional half-normal detection function (Borchers and Efford 2008, Royle et al. 2014) to model the probability p of detecting individual i at detector j as a decreasing function of the distance d between the detector and the individual's center of activity s_i : $p_{ij} = p_{0ij} \exp(-d_{ij}^2 / 2\sigma^2)$. The detection function is assumed to reflect individual space use and is therefore directly linked with the home range concept (Royle et al. 2014). Because we used a data-augmentation approach (Royle et al. 2007), the detection of an individual is conditional on the individual's state z_i ($z_i=1$ when individual i is member of the population N), which is governed by the inclusion probability ψ : $z_i \sim \text{Bernoulli}(\psi)$. The population size can be then derived by summing the z_i 's: $N = \sum_{i=1}^M z_i$, where M is the chosen size of the data-augmented population (Royle et al. 2007) and represents the maximum number of wolverines in the habitat S (Ecological submodel).

In our study, detectors are the centers of 5572 10×10 km grid cells, covering a land area extending 100 km beyond the outermost wolverine NGS detections collected during the sampling period (Supporting information). We used a partially aggregated binomial observation model (Milleret et al. 2018) to retain more information from the wolverine NGS data by dividing each main detector cell into 25 subdetector cells of 2×2 km. By retrieving the number of subdetector cells with at least one noninvasive sample for each wolverine detected at each main detector cell, we generated individual spatial detection histories (Royle et al. 2014). Finally, we placed a 40 km buffer around the detector grid to define the habitat S . This value was chosen based on the average home-range radius of adult Scandinavian wolverines (Persson et al. 2010, Mattisson et al. 2011, Aronsson et al. 2022), so that the buffer is larger than three times the estimated σ of 10.3 km (95% Bayesian credible interval [CI] = 10.1–10.5 km) for male wolverines, as reported by Bischof et al. (2020). This buffer area allows detection of individuals even if their activity centers are located outside the detector grid (Efford 2004, 2011). The detector grid covered most of the contiguous Scandinavian Peninsula over Norway and Sweden ($58^{\circ}08' - 70^{\circ}42'N$, $5^{\circ}56' - 32^{\circ}46'E$, Supporting information), while parts of the buffer (41.6%) fell inside Finland and Russia. Thus, the available habitat was 633 200 km², after removing large lakes and other noncontiguous land areas, of which 88% (557 200 km²) were in Norway and Sweden (Supporting information).

Wolverine NGS was conducted by hundreds of field staff and volunteers across different jurisdictions in Norway and

Sweden. We therefore expected spatial variability in detection probability of wolverine individuals (Efford et al. 2013, Moqanaki et al. 2021). Following Bischof et al. (2020), we considered a different baseline detection probability for each jurisdiction $p_{0_{\text{County}}}$ (County = 1, 2, ..., 8) to account for possible regional differences in monitoring regimes. Jurisdictions were defined based on carnivore management regions in Norway and counties in Sweden (Bischof et al. 2020), with slight modifications to match our habitat extent (Supporting information). We merged neighboring jurisdictions to ensure sufficient wolverine detections for estimating baseline detection probability in each unit (Bischof et al. 2020). In addition, we modeled the effect of three detector and one individual-level covariates that may influence the probability of wolverine detection (Supporting information):

$$\text{logit}(p_{0_{ij}}) = p_{0_{\text{County}_j}} + \beta_E \text{Effort}_j + \beta_R \text{Road}_j + \beta_S \text{Snow}_j + \beta_P \text{Previous}_i \quad (1)$$

Effort_{*j*} is the number of track points per 500 m of GPS search tracks within each detector grid cell *j* recorded during the structured NGS, **Road**_{*j*} is the logarithm of the average geographic distance (km) from each detector to the nearest road of any type, and **Snow**_{*j*} is the average percentage of snow-covered land in each detector grid cell during the sampling months (December 2018–June 2019, Supporting information). We also modeled individual variation linked with detection in the previous monitoring season **Previous**_{*i*}; a binary covariate which takes the value 1 if individual *i* was detected in the previous monitoring season and 0 otherwise. During NGS, investigators are believed to have the tendency to prioritize searching in locations where their searches were previously successful, which could positively influence the detection probability of those previously detected wolverine individuals during the focal monitoring season (Gervasi et al. 2014, Milleret et al. 2022). Availability of the monitoring data from the previous year made it possible to account for this potential source of heterogeneity in wolverine detectability. This individual binary covariate **Previous**_{*i*} is latent for augmented individuals and was modeled following a Bernoulli distribution: $\text{Previous}_i \sim \text{Bernoulli}(\pi)$, where π is the probability that an arbitrary individual from the population was detected in the previous year. All continuous spatial covariates were scaled before SCR model fitting. See Supporting information for further details on detection covariates, the rationale to include them, and their original source and spatial depiction.

The ecological submodel

The ecological submodel describes the number and distribution of all wolverines present in the population (i.e. detected and nondetected). We used a data augmentation approach (Royle et al. 2007) to account for those wolverine individuals that were not detected during NGS, where the superpopulation size *M* (i.e. detected and augmented individuals) was chosen to be considerably larger than *N*. Following

Bischof et al. (2020), and given the relatively high detectability of the target population during NGS (Milleret et al. 2022), we chose an augmentation factor of 0.8 to facilitate the analysis by Markov chain Monte Carlo (MCMC). Thus, *M* was large enough, such that the probability that *M* individuals were alive in *S* during NGS was negligible.

SCR estimates of abundance are spatially explicit, meaning that they are derived from the estimated location of all individual activity centers *s_i* with *z_i* = 1 across the available habitat *S* (Efford 2004, Borchers and Efford 2008, Royle et al. 2014). The collection of activity centers can be seen as the realization of a statistical point process (Illian et al. 2008). To study how wolverine density varies in Scandinavia in response to a number of environmental and history-related covariates (Table 1, Supporting information), we used an inhomogeneous binomial point process to model spatial variation in the distribution of individual activity centers with intensity function (Zhang et al. 2023): $\lambda(s) = e^{\beta \mathbf{X}(s)}$, where $\mathbf{X}(s)$ is a vector of spatial covariate values evaluated at location *s*, and β is a vector of associated regression coefficients. The intensity function λ conditions the placement of activity centers within each of the 20 × 20 km habitat grid cells *s* used in this analysis (Supporting information). In this formulation, no intercept is needed, as the number of activity centers is conditioned by data augmentation; thus, regression coefficients represent the relative effects of the different covariates on wolverine density (Zhang et al. 2023).

To disentangle the determinants of wolverine density within Scandinavia, we measured habitat characteristics at the scale of the home range of a wolverine (i.e. the second-order of habitat selection; Johnson 1980). We selected biotic and abiotic covariates following previous studies on wolverine distribution and habitat use and preferences (Fisher et al. 2022, Table 1). Specifically, we selected covariates that may explain spatial variation in wolverine density in Scandinavia at broad scale (Table 1, Supporting information): 1) distance from the relict range (Landa et al. 2000, Flagstad et al. 2004, Fig. 1) to describe recolonization history, 2) Terrain Ruggedness Index (TRI), explaining general topographic complexity, 3) average percentage of year-round snow-covered land as a measure of climate suitability (which was different from the snow covariate used as a detector-level covariate, Supporting information), 4) percentage of forest cover, representing land use and habitat productivity, 5) moose *Alces alces* harvest density as a proxy of wild prey biomass availability, 6) percentage of human settlement areas as a measure of human density and associated disturbances, and 7) zonal management to account for regional differences in wolverine management plans and other large-scale environmental conditions.

The impact of current management was specifically included because of unique management goals for wolverines in different areas of Norway and Sweden (Ministry of the Environment 2003, Naturvårdsverket Årenden 2020). Briefly, we divided our habitat layer into northern and southern zones in each country (i.e. four zones, Table 1, Supporting information) by aggregating jurisdictions with similar management goals for the number of wolverine annual reproduction and other

Table 1. Description, rationale for inclusion, expected effects, and source and native spatial resolution of covariates of density used to model the density distribution of the wolverine *Gulo gulo* across Norway and Sweden between December 2018 and June 2019

Covariate	Description and rationale	Effects	Resolution and source
Relict (X_1)	Distance (m) from the relict range represents the founding population and colonization history. The relict range describes roughly the area occupied by the Fennoscandian wolverine population at its lowest point in modern times (Landa et al. 2000, Flagstad et al. 2004, Chapron et al. 2014, Lansink et al. 2020)	–	Calculated using the wolverine's geographic distribution range in the 1970s as reported by Landa et al. (2000). All 20 × 20 km habitat cells falling within the relict range area were assigned a value of zero. We then computed the Euclidean distance for all habitat cells to the nearest cell with a value of zero using the <i>distance</i> function of the R package 'raster' (www.r-project.org, Hijmans 2021)
Ruggedness (X_2)	Terrain Ruggedness Index (TRI) is the mean of the absolute elevation differences between the value of a habitat cell and the value of its eight surrounding cells (Wilson et al. 2007). TRI represents topographic complexity, refuge availability, and level of human disturbances (May et al. 2008, 2012, Rauset et al. 2013, Poley et al. 2018)	+	Obtained through the <i>terrain</i> function of the R package 'terra' (www.r-project.org, Hijmans et al. 2022) using an elevation layer (Amazon Web Services Terrain Tiles and OpenTopography global data sets Application Programming Interface) at about 256 × 256 m obtained via the <i>get_elev_raster</i> function of the R package 'elevatr' (www.r-project.org, Hollister et al. 2021)
Snow (X_3)	The average percentage of year-round snow cover across years 2008–2019, representing climate severity, denning suitability, and prey availability and vulnerability to predation (Copeland et al. 2010, May et al. 2012, Aronsson and Persson 2017, Lukacs et al. 2020, Mowat et al. 2020, Barrueto et al. 2022)	+	Calculated using monthly maps of the percentage of snow-covered land based on the MODIS/Terra Snow Cover Daily L3 Global 500 m Grid data set (www.neo.sci.gsfc.nasa.gov)
Forest (X_4)	Percentage of forest cover was a measure of land use, habitat productivity, greater wild prey availability, and cover (May et al. 2006, 2008, Inman et al. 2012, Scrafford et al. 2017, Cimatti et al. 2021)	+	Obtained using the European Space Agency–Climate Change Initiative Land Cover project (categories 50, 60, 61, 62, 70, 71, 72, 80; www.esa-landcover-cci.org) at about 176 × 176 m
Moose (X_5)	An index of moose <i>Alces alces</i> density using hunting bags, representing habitat productivity and a proxy for wild prey biomass (Van Dijk et al. 2008, Mattisson et al. 2016, van der Veen et al. 2020)	+	Calculated at 2 × 2 km resolution using the number of moose harvested/km ² at the level of municipalities and hunting management units in Norway and Sweden, respectively (Statistisk sentralbyrå 2021, Ålgdata 2021a, b). We used data from the previous hunting season (September–October 2017), as suggested by Ueno et al. (2014). Because of a lack of data from the buffer area in Finland and Russia, we replaced missing values with mean values of the 48 neighborhood cells using the <i>focal</i> function of the R package 'raster' (www.r-project.org, Hijmans 2021)
Settlements (X_6)	The percentage of ground surface covered by human settlements was a proxy for human population density and associated disturbances (May et al. 2006, Lukacs et al. 2020, Cretois et al. 2021, Barrueto et al. 2022)	–	Downloaded at 57 m resolution from the World Settlement Footprint data set (WSF2015; Marconcini et al. 2020) and log transformed after adding a value of one to deal with zero values
Zonal management (R_1, \dots, R_4)	An aggregation of administrative units (i.e. large carnivore management regions in Norway and counties in Sweden) with shared population goals for the wolverine (Ministry of Environment 2003, Naturvårdsverket Årendenr 2020), representing regional variation in management strategies and other region-specific environmental conditions (Persson et al. 2009, Hobbs et al. 2012, Morehouse and Boyce 2016, Aronsson and Persson 2017, Kortello et al. 2019, Barrueto et al. 2020)	+/-	Counties in Sweden and carnivore management regions in Norway within 1) northern zones with the management goal of 10 or more annual wolverine reproductions: 1a) Norrbotten, Västerbotten, and Jämtland (Sweden), plus a small fraction of the buffer and 1b) management region 8 (Finnmark and Troms), region 7 (Nordland), and region 6 (Trøndelag and Møre og Romsdal) in Norway; 2) southern zones with the management goal of < 10 annual wolverine reproductions: 2a) Västernorrland, Dalarna, Gävleborg, and Värmland, plus a small part of the neighboring counties without management goals: Västmanland, Västra Götaland, and Örebro (Sweden) and 2b) management region 5 (Hedmark) and region 3 (Oppland), plus a small part of the neighboring counties without management goals: Sogn og Fjordane, Hordaland, Rogaland, Vest-Agder, Aust-Agder, Telemark, Buskerud, and Vestfold (Norway)

environmental conditions (e.g. climate, prey availability and abundance, and human influence). We simplified the spatial variation in wolverine management by merging several counties or carnivore management regions, and partially included jurisdictions in the southern part of each country without management goals (Table 1, Fig. 1), because these southern counties contained no NGS and wolverine detections in our data set (Supporting information). Likewise, we merged the buffer area in neighboring Finland and Russia with the northern zones (Supporting information). We then calculated the proportion overlap between each habitat cell and the resulting four zones to define four spatial covariates (Supporting information). Because the four proportions sum to one, we did not use the first zone covariate to avoid identifiability issues (i.e. the northern zone in Sweden, zone 1a in Table 1, was an implicit intercept). Activity center placement reflects environmental configuration throughout the home range, not just at one location. Thus, discrete changes in conditions (e.g. management) from one side of a border to another can lead to artificial behavior in the model when using cell-based covariate values. To achieve a more realistic scale of home range placement in the model, we averaged covariate values of the four management zones using a moving window (Table 1). This created gradual transitions between regions (Supporting information). Because management goals and other zone-specific characteristics of the biotic and abiotic environment may also have affected the wolverine's ability to recolonize away from the relict range, we included an interaction term between the distance from the relict range and each of the four zones:

$$e^{\lambda(s)} = \sum_{r=2}^4 \{\beta_{R_r} \mathbf{R}_r(s) + \beta_{R_r X_1} \mathbf{X}_1(s) \mathbf{R}_r(s)\} + \sum_{c=1}^6 \beta_{X_c} \mathbf{X}_c(s) \quad (2)$$

The six spatial covariates \mathbf{X}_c are the distance from the relict range \mathbf{X}_1 , Terrain Ruggedness Index \mathbf{X}_2 , the average percentage of year-round snow cover \mathbf{X}_3 , the percentage of forest cover \mathbf{X}_4 , the percentage of human settlement areas \mathbf{X}_5 , and the moose harvest density \mathbf{X}_6 . \mathbf{R}_2 , \mathbf{R}_3 , and \mathbf{R}_4 are the three zone covariates representing southern Sweden and northern and southern Norway (Table 1). In total, we estimated 12 regression coefficients β (Supporting information).

We transformed all covariate raster layers from the original projection to the Universal Transverse Mercator (UTM zone 33N) and locally interpolated the raster values using the 'bilinear' method of the *resample* function of the R package 'raster' (www.r-project.org, Hijmans 2021) to match the 20 × 20 km habitat grid used in this analysis (Supporting information). All continuous covariates were then standardized prior to their inclusion in the model to have a mean of zero and one unit standard deviation. Correlation among the covariates was generally low (Pearson's correlation coefficient $r \leq 0.62$). Further details regarding the rationale for including each covariate, their sources, and their expected effects are provided in Table 1, and the Supporting information provides their spatial depiction and mean and SD of the values.

Implementation

We fitted SCR models with NIMBLE (ver. 0.12.2, de Valpine et al. 2022) in R (ver. 4.2.1, www.r-project.org) for female and male wolverines separately, using the recent developments by Turek et al. (2021) and custom functions made available through the R package 'nimbleSCR' (www.r-project.org, Bischof et al. 2021). We ran four MCMC chains, each with 200 000 iterations, discarded the initial 10 000 samples as burn-in, and thinned by a factor of 10 for creating the density maps. We assessed mixing of chains by inspecting traceplots, and we considered models as converged when the potential scale reduction value \hat{R} was ≤ 1.10 for all parameters (Brooks and Gelman 1998). See Supporting information for data and R code (www.r-project.org) for fitting the SCR model and the list of priors.

To explore the relative importance of each covariate on density, we incorporated a Bayesian variable selection approach in NIMBLE using reversible jump MCMC with indicator variables (Green 1995, O'Hara and Sillanpää 2009). We incorporated an indicator variable w associated with each regression coefficient β ($n=12$, Supporting information). Thus, we modified Eq. (2) to include ($w=1$) or exclude ($w=0$) the effect of each coefficient in the presence of other covariate effects in a given posterior draw: $\lambda(s) = e^{\beta_1 w_1 X_1(s) + \dots + \beta_p w_p X_p(s)}$. We constrained inclusion of the interaction coefficients to when the corresponding main effects were also included. For inference on the different coefficients, we discarded MCMC draws where $w=0$.

We calculated the median and the 95% CI limits of the posterior distribution for all parameters, except for abundance, where we reported mean and 95% CI. To obtain total wolverine abundance, we combined N estimates of male and female wolverines by merging posterior MCMC samples from the sex-specific SCR models. In both total and sex-specific models, we summed the total number of predicted activity center locations of alive individuals ($z_i=1$) within each habitat cell for each iteration of the MCMC chains; thus, we generated a cell-based posterior distribution of abundance that can be viewed also as density. Using this approach, we extracted abundance and density estimates and the associated uncertainty for different spatial units relevant for wolverine management at the country level, besides the total estimates for the entire population in Norway and Sweden.

We constructed two types of sex-specific density maps: 1) a realized density map based on the posterior location of activity centers as described above, and 2) an expected density map based on the estimated intensity of the density point process per habitat cell of 20 × 20 km and the estimate of population size: $\mathbf{D}_{\text{exp}}(s) = N\lambda(s) / \sum_{s=1}^S \lambda(s)$. 'Realized' density maps show density based on the average model-estimated activity center locations of individuals, as opposed to 'expected' density maps, which show predicted density based on the regression model underlying the intensity surface. To present uncertainty, we calculated and mapped the standard deviation of the per cell posterior of density (Miller et al. 2013). We used all MCMC samples to construct the density maps, regardless of the indicator variable values.

Results

Noninvasive genetic sampling

During the sampling period between 1 December 2018 and 30 June 2019, 283 282 km of GPS search tracks were recorded within our designated detector grid (Supporting information) across Norway (34%) and Sweden (66%). The final NGS data set consisted of 2444 (1350 male and 1094 female) detections from 742 (335 male and 407 female) genetically identified wolverine individuals across the entire population on the Scandinavian Peninsula (Supporting information). The number of detections (i.e. recaptures) per identified individual ranged from 1 to 13 for both sexes (mean = 3.0 males and 2.1 females).

Density predictors

The variation in wolverine density across Scandinavia was explained by distance from the relict range in different zones, human settlement areas, moose density proxy, year-round snow, terrain ruggedness, and forest cover (Fig. 2). The magnitude of the effects and uncertainty around them varied moderately between the sexes (Fig. 2). For both females and males, the effects of being in southern Norway, distance from the relict range in northern Sweden, and percentage of human settlements received the most support based on the inclusion probability (≥ 0.99 ; Fig. 2). In addition, for female wolverines, the effects of being in northern Norway and distance from the relict range in southern Norway and, for males, the effect of moose density proxy received inclusion probabilities of ≥ 0.99 (Fig. 2). See Supporting information for the most supported SCR models for each sex.

Among the covariates considered, percentage of human settlement areas had the largest negative effects on both female and male wolverine densities (median and 95% CI $\beta_{X_5} = -1.61, -2.66$ to -0.79 [female] and $-2.27, -3.41$ to -1.33 [male]; Fig. 2). Likewise, distance from the relict range negatively affected the density of both sexes, with significantly stronger effects in southern Norway ($\beta_{R_4 X_1} = -1.35, -1.99$ to -0.70 [female] and $-1.07, -1.87$ to -0.26 [male]), compared to the effect of distance from the relict range in northern Sweden (Fig. 3). Based on our results, we predicted that areas located 30 km away from the relict range (as the crow flies) would have expected wolverine densities on average about two-thirds lower in the southern zones of Norway and Sweden compared to the northern zones (Fig. 3). Moose density was positively associated with both female and male wolverine densities ($\beta_{X_6} = 0.19, 0.02$ – 0.35 [female] and $0.46, 0.31$ – 0.63 [male]; Fig. 2). The effects of forest cover ($\beta_{X_4} = 0.32, 0.12$ – 0.52) and terrain ruggedness on density was significantly positive for female wolverines only ($\beta_{X_2} = 0.42, 0.25$ – 0.59), while the effect of year-round snow cover was positive for males only ($\beta_{X_3} = 0.35, 0.11$ – 0.56 ; Fig. 2).

Detection predictors

The effects of detection covariates varied slightly between male and female wolverines (Supporting information). Baseline detection probability p_0 was comparable between sexes (median and 95% CI $p_0 = 0.02, 0.01$ – 0.02 for both males and females), but varied moderately among the eight carnivore management regions and counties in Norway and Sweden, respectively (Supporting information). Both female and male wolverine detection probabilities increased with search effort ($\beta_E = 0.62, 0.53$ – 0.71 [female] and $0.51, 0.44$ – 0.59 [male]). Further, for female wolverines, searching farther away from the nearest road increased their detectability ($\beta_R = 0.19, 0.07$ – 0.31). Higher percentage of snow cover during the sampling months decreased detectability of males ($\beta_S = -0.22, -0.37$ to -0.08). The individual-level covariate representing wolverine detection in the previous sampling year positively influenced male wolverine detectability only ($\beta_P = 0.61, 0.44$ – 0.77), suggesting sex-specific detection bias during NGS. The spatial scale parameter was greater for males ($\sigma_m = 8$ km, 7.6 – 8.2) than for females ($\sigma_f = 6$ km, 5.6 – 6.4). See Supporting information for more details.

Sex-specific and total estimates of abundance and density

We estimated the abundance of the Scandinavian wolverine population within our detector grid (Supporting information) during the 2018/2019 monitoring season at 408 (95% CI = 397–420) males and 667 (95% CI = 640–697) females. The wolverine population in Sweden was estimated to be between 640 and 692 individuals, while in Norway we estimated between 397 and 425 wolverines (Supporting information). Overall, we predicted higher wolverine densities for both males and females closer to the relict range, but the pattern was more pronounced for females (Fig. 4).

Discussion

The present spatial configuration of wolverine density across the Scandinavian Peninsula reflects the species' recovery from past range contraction and population decline, modulated by current management and environmental conditions. The importance of the relict range along the Swedish–Norwegian border highlights the need for coordinated monitoring and management of this transboundary population of wolverines. Monitoring is already coordinated to some extent (Gervasi et al. 2016, 2019, Bischof et al. 2020), but fully coordinated management is made difficult by existing differences in national and regional population goals and legal obligations, which are also tied to differences in the intensity of conflict.

The ghosts of the past

A key driver of current wolverine density distribution for both sexes in Norway and Sweden appears to be distance

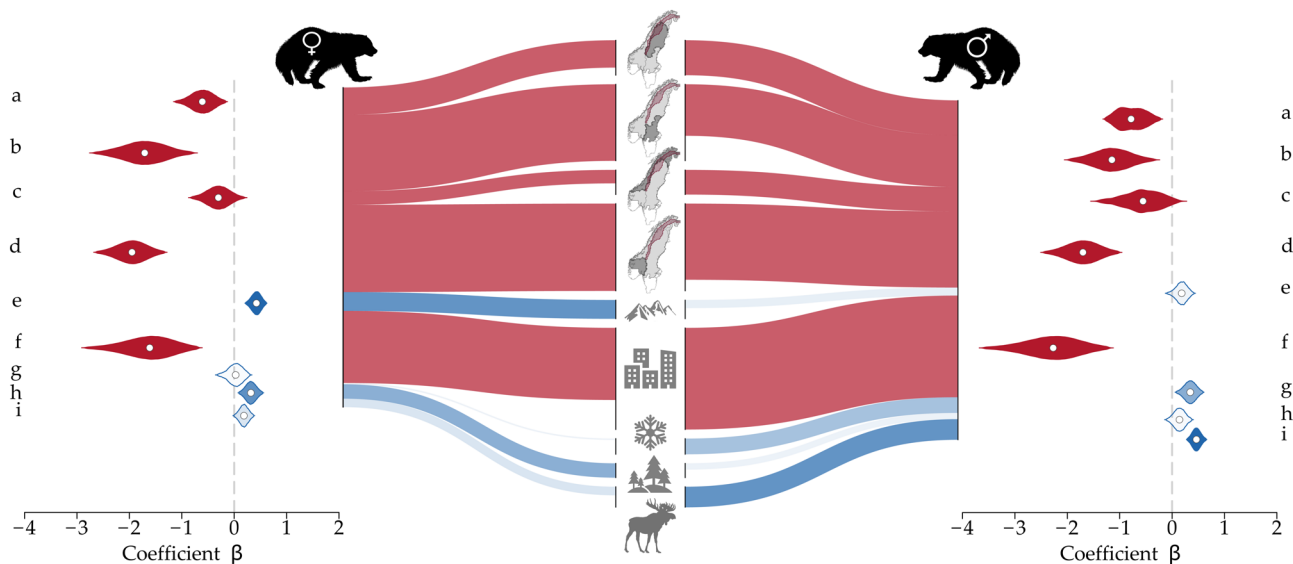


Figure 2. The effect of environmental covariates on density of female (left) and male (right) wolverines *Gulo gulo* in the Scandinavian Peninsula between December 2018 and June 2019. The covariates of density are (from top to bottom): Distance from the relict range in (a) northern Sweden, (b) southern Sweden, (c) northern Norway, (d) southern Norway, (e) Terrain Ruggedness Index, (f) human settlement index, (g) year-round snow cover, (h) forest cover, and (i) moose *Alces alces* harvest density (Table 1). All continuous covariates were standardized prior to their inclusion in the models. Zone-specific intercepts are not shown (Supporting information). The violins show median (white dots) and 95% Bayesian credible interval limits of regression coefficients β estimates, where effect sizes are on an exponential scale. Line widths represent the magnitude of the median effect (i.e. the thicker, the larger the strength of the covariate effects). Line and violin colors show direction of the effects (blue = positive and red = negative effects), and the opacity level indicates the inclusion probability (0 [transparent] to 1 [opaque]; Supporting information). For the four zone-specific effects of distance from the relict range (a–d), inclusion probabilities are based on the inclusion probability of the distance effect in northern Sweden (a).

from the relict range (Fig. 1, Supporting information), where Scandinavian wolverines survived human persecution before their legal protection in the 1970s (Landa et al. 2000, Flagstad et al. 2004). We also found that zonal management is one of the main drivers of wolverine density in Scandinavia (Fig. 3). The density of both male and female wolverines declines with increasing distance from the relict range, and the rate of decline further varies among zones with contrasting management goals regarding wolverine annual reproduction (Fig. 2, 3). Regional differences in the effect of distance from the relict range is likely a sign that the current recolonization of wolverines is both a function of past and current management practices and environmental conditions. Together, these factors explained much of the spatial variation in current density of wolverines in the Scandinavian Peninsula (Fig. 4). Whether the relict range represents a highly suitable habitat for the Scandinavian wolverine (i.e. historical and current core) or the species was pushed into the alpine refuge areas during the peak of the persecution is not fully understood (Flagstad et al. 2004, Kerley et al. 2012, Zigouris et al. 2013). Nonetheless, wolverine recolonization in Scandinavia matches the general pattern of return of other large carnivore species in Western Europe and North America (Linnell et al. 2001, Chapron et al. 2014). Successful recovery of these species is partially attributed to changing public attitudes towards large carnivores and effective law enforcement which, in turn, have lowered the risk of direct

killing by humans (Zedrosser et al. 2011, Ingeman et al. 2022). Likewise, increasing tolerance towards wolverines by Scandinavian farmers and herders has in part been achieved through intensive zonal management of wolverines and compensation schemes (Persson et al. 2015, Aronsson and Persson 2017, Strand et al. 2019). Balancing the landscape-level requirements of a viable wolverine (meta-)population and human interests will therefore remain crucial for successful management.

The ability of wolverines to travel long distances has probably contributed to their successful recolonization in part of their historical range in Scandinavia. Male wolverines are more likely to disperse, whereas females usually stay close to their natal range and show high home-range fidelity (Inman et al. 2012, Packila et al. 2017, Aronsson and Persson 2018). We found that spatial covariates tested in our study had qualitatively similar effects on the density of female and male wolverines (Fig. 2). We note that male and female Scandinavian wolverines have a comparable level of human-induced mortality (Bischof et al. 2020, Milleret et al. 2022). Additionally, long-distance dispersal events that lead to successful colonization of unoccupied habitat are not common (Flagstad et al. 2004, Packila et al. 2017). Even if male wolverines on average disperse farther, they may not always successfully establish significantly farther than females. Nonetheless, we observed pockets of higher expected male wolverine density farther from the relict range compared to

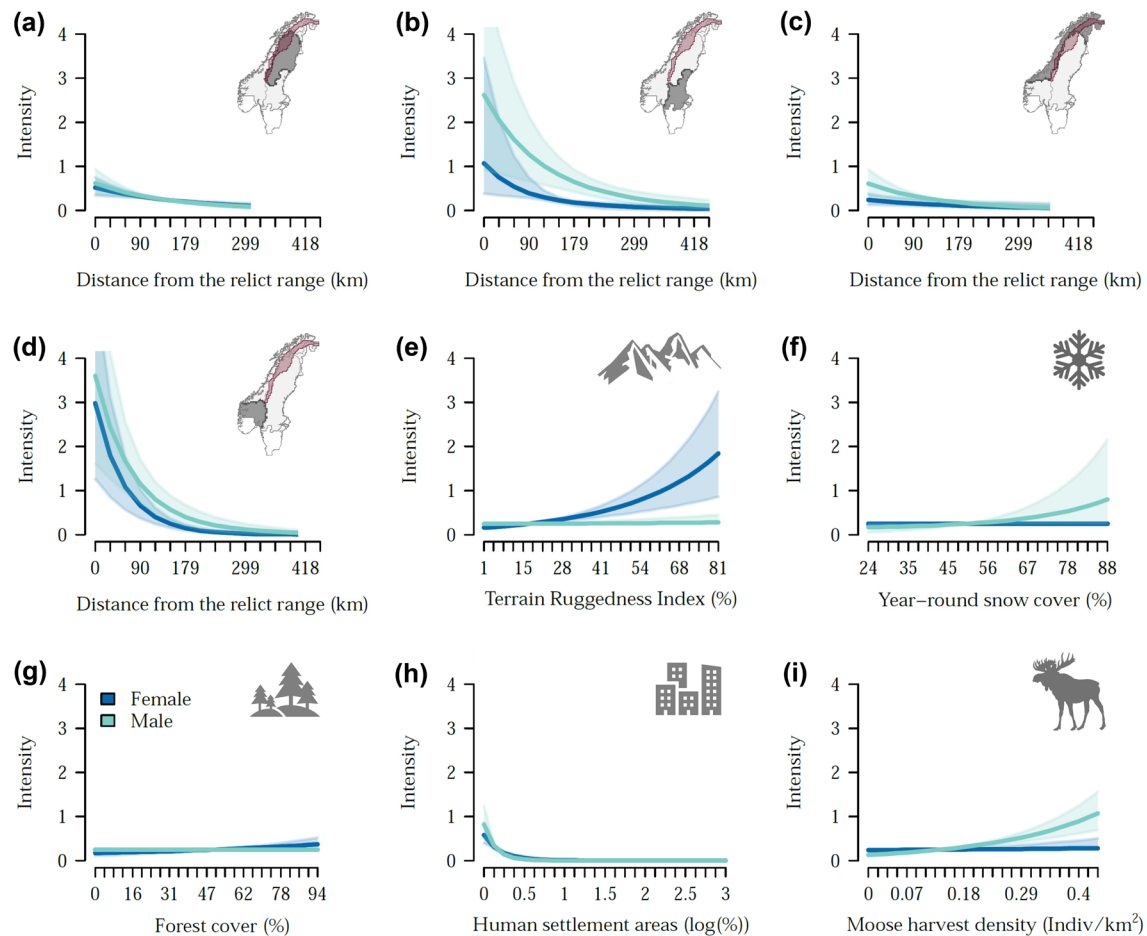


Figure 3. Expected intensity of the density point process for female (blue) and male (green) wolverines *Gulo gulo* in Norway and Sweden as a function of environmental covariates included in this study. Mean response and 95% Bayesian credible interval limits are represented by thick lines and transparent polygons, respectively. Predictions in plots (a)–(d) are for the range of values of distance from the relict range (km) that was available in the given zone: (a) northern Sweden; (b) southern Sweden; (c) northern Norway; and (d) southern Norway. The red polygons in the small maps (a)–(d) indicate the relict range (Fig. 1), and the dark gray polygons are different zones with contrasting management goals and environmental conditions for the wolverine across the available habitat (Supporting information). The intensity of the point process reflects the relative distribution of individual activity centers. For example, twice as many individuals are expected to have their activity centers located in a cell with an intensity of two compared to one.

the expected female density, which remained the highest in and near the relict range (Fig. 4). This pattern was reflected in the sex-specific estimates of the effect of distance from the relict range in the southern zones of Sweden and Norway (Fig. 2).

We estimated, on average, substantially lower wolverine densities in the southern zones of Norway and Sweden compared to the northern zones (Fig. 3). The southern zones generally do not cover semidomesticated reindeer husbandry areas and calving grounds, but the southern zone in Norway includes areas with free-ranging domestic sheep. The current management strategy in both countries allows more wolverine annual reproduction in the northern zones (Ministry of the Environment 2003, Naturvårdsverket Årendenr 2020), and the legal removal of wolverines is proportionally more intense in the south, especially in southwestern Norway, to protect the free-ranging sheep (Strand et al. 2019). No

wolverines are currently tolerated in southwestern Norway. There are also mismatches between the management goals, their implementation, and regional tolerance of the wolverine in Scandinavia (Aronsson and Persson 2017, Gervasi et al. 2019) that are not entirely reflected by the four zones we considered. Thus, it is likely that the combined effect of the higher cost of dispersal from the relict range and the current management plans regarding wolverine recolonization, together with region-specific environmental characteristics, have resulted in slower wolverine expansion and lower densities in the southern parts of the Scandinavian Peninsula.

Population-level drivers of variation in density

Wildlife distributions and densities are continuously being shaped by multiple factors at different spatio-temporal scales. Abiotic factors, such as temperature and precipitation, play

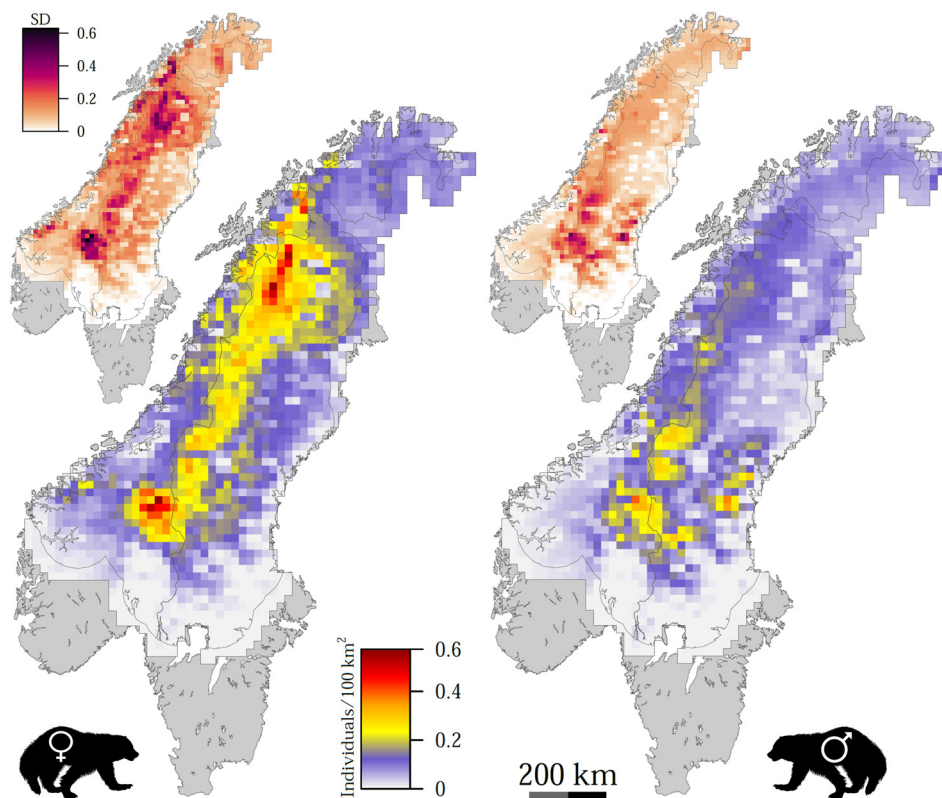


Figure 4. Expected density surfaces of female (left) and male (right) wolverines *Gulo gulo* in Norway and Sweden as a function of environmental covariates included in spatial capture-recapture analysis (Table 1). The main maps show the average expected density surfaces for each sex (individuals per 100 km²) and smaller inset maps show the cell-based standard deviation of predictions.

a key role in shaping species distributions at broad scales (Benton 2009). There is also increasing evidence that biotic factors are important determinants of species distributions at both local and large spatial extents, particularly when accounting for interacting drivers (Van der Putten et al. 2010, Wisz et al. 2013). We found that current environmental features that describe landscape heterogeneity and productivity can explain variation in the Scandinavian wolverine density at the landscape level. Although the relative importance of some of these covariates varied between sexes (Fig. 2), anthropogenic factors had a consistently negative impact on both male and female wolverine density. Studies from the Nearctic range of the wolverine have also shown that drivers associated with anthropogenic disturbances can be more important than the traditionally held drivers of wolverine density, such as topographic ruggedness and snow cover (Fisher et al. 2013, Heim et al. 2017, Chow-Fraser et al. 2022). Besides quantifying the driving factors of density for the entire population of the Scandinavian wolverines, our study advances the previous findings (Fisher et al. 2022 and references in Table 1) by highlighting the role of past persecution history and current management practices in modulating natural recolonization across a human-dominated landscape.

Human-caused mortality and anthropogenic fragmentation of habitat are limiting wolverine distribution and density

globally (May et al. 2006, Persson et al. 2009, Fisher et al. 2013, Mowat et al. 2020, Lukacs et al. 2020, Lansink et al. 2022, Barrueto et al. 2022). Within the Scandinavian large carnivore guild, wolverines are believed to be the most sensitive to habitat fragmentation (May et al. 2008). We included the percentage of human settlement areas as a measure of human pressure on the natural environment (Marconcini et al. 2020), which represents human population density and the associated disturbances. The negative impact of human settlements on wolverine density appeared to be substantial (Fig. 2), and we observed drastic declines in the expected density of both male and female wolverines with increasing human settlements (Fig. 3). In Norway and Sweden, the majority of large towns with the highest concentration of permanent human settlements and high traffic-volume roads are located in the southern parts. Likewise, the farthest distance from the relict range and zones with lower annual wolverine reproduction goals are also in the south (Fig. 3, Supporting information). Thus, the combined effect of all these anthropogenic factors, as well as the zero tolerance towards wolverines in southwestern Norway, have probably limited the wolverine density distribution in the southern parts of the Scandinavian Peninsula. Nonetheless, the south represents the wolverine population's expansion front, and the observed latitudinal pattern may also be explained by the observation

that wildlife population dynamics can differ considerably from the core areas (Swenson et al. 1998, Burton et al. 2010, Angert et al. 2020). With increasing human-made barriers to wolverine movement and dispersal (Aronsson and Persson 2018, Sawaya et al. 2019, Lansink et al. 2022), we expect the resulting population fragmentation will also play a major role in shaping the distribution and dynamics of the Scandinavian wolverine population in the future.

As a measure of wild prey biomass availability, we included moose harvest density in our models (Table 1, Supporting information). We estimated significantly higher wolverine densities in areas with higher moose harvest density, and this positive effect was more pronounced for males (Fig. 3). Wolverines are generally facultative scavengers and, in many areas of Fennoscandia, they depend on slaughter remains from hunting and carcasses of prey killed by other top predators, including the Eurasian lynx *Lynx lynx*, wolf *Canis lupus*, and brown bear *Ursus arctos*, as well as animals dead from natural causes and roadkills (Van Dijk et al. 2008, Mattisson et al. 2011, Koskela et al. 2013, Aronsson et al. 2022). Moose occurs throughout the wolverine range in Scandinavia and moose carrion is an important food source for wolverines in many areas (Van Dijk et al. 2008, Mattisson et al. 2016, Aronsson et al. 2022), especially for breeding females (Koskela et al. 2013) and during winter (October–April) that overlaps with our study period. There is, however, considerable spatial and temporal variation in wolverine diet in Scandinavia, with reindeer as the most important prey for wolverines in some areas (Mattisson et al. 2016). Unfortunately, we were unable to find comprehensive and reliable data on the density of wild or semidomesticated reindeer across the entire Scandinavian Peninsula to be considered for our study.

The positive effects of terrain ruggedness and the percentage of forest cover on wolverine density were significant for females only, whereas the average percentage of year-round snow appeared to only impact male density (Fig. 2). Until recently, Scandinavian wolverines were not considered to be a forest-dwelling species, as they appeared to select open and rugged terrain at higher elevations with snow, away from human activity (May et al. 2008, 2012, Rauset et al. 2013). Spring snow cover in particular is believed to be important for reproducing females, because it determines denning suitability and offspring survival (Copeland et al. 2010, Mowat et al. 2020, Barrueto et al. 2022). However, in recent years, the Scandinavian wolverine population has expanded considerably into the boreal forest and has now colonized areas without persistent spring snow cover (Aronsson and Persson 2017). We chose the average year-round snow cover during the past decade not to specifically account for denning suitability for the wolverine, but as a measure of climatic niche suitability that may have shaped the wolverine's density distribution today (Table 1). Terrain ruggedness and forest cover probably correlate with the degree of past persecution due to accessibility and history of land protection (Joppa and Pfaff 2009, Kerley et al. 2012) and the significance of these covariates for female wolverines may then

reflect their affinity for high-quality habitat compared to males (May et al. 2008, 2012, Rauset et al. 2013, Aronsson and Persson 2018).

Wolverines in the past, present, and future

Scandinavian wolverines have recovered from the brink of extinction and are now occupying a considerable portion of their historic range (Flagstad et al. 2004, Chapron et al. 2014, Aronsson and Persson 2017, Gervasi et al. 2019, Bischof et al. 2020). The effects of past impacts are nonetheless still clearly visible today, modulated but not masked by current environmental conditions and management regimes. The wolverine density in Scandinavia is shaped by human interests, while interacting with the history of local extinction. Wolverines are also impacted by other environmental covariates, several of which are directly or indirectly influenced by humans (e.g. prey base, land use and climate conditions). In an increasingly human-dominated landscape, the impact of humans on wolverines is likely to be even greater in the coming decades, further defining the state of the Scandinavian wolverine population. Despite the expansion of wolverines (Chapron et al. 2014, Gervasi et al. 2019), an increasing human impact, if neglected, may therefore eventually again limit wolverines to the relict range that served as a refuge in the past.

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Author contributions

Ehsan Moqanaki: Conceptualization (equal); Formal analysis (lead); Investigation (lead); Methodology (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Cyril Milleret:** Formal analysis (supporting); Methodology (supporting); Validation (supporting); Writing – review and editing (supporting). **Pierre Dupont:** Formal analysis (supporting); Methodology (supporting); Validation (supporting); Visualization (supporting); Writing – review and editing (supporting). **Henrik Brøseth:** Data curation (lead); Investigation (supporting); Validation (supporting); Writing – review and editing (supporting). **Richard Bischof:** Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Investigation (supporting);

Methodology (supporting); Project administration (lead); Supervision (lead); Validation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

Transparent peer review

The peer review history for this article is available at <https://publons.com/publon/10.1111/ecog.06689>.

Data availability statement

Wolverine detections used in this study are available through the database Rovbase ver. 3.0 at www.rovbase.no or www.rovbase.se. Data and R scripts of the spatial capture-recapture analysis are available from the Zenodo Digital Repository: <https://doi.org/10.5281/zenodo.7997915> (Moqanaki 2023).

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.n2z34tn29> (Moqanaki et al. 2023).

Supporting information

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

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