

1 **Running Head:** Wolverine density determinants in Scandinavia

2

3 **Wolverine density distribution reflects past**
4 **persecution and current management in**
5 **Scandinavia**

6 Ehsan Moqanaki^{1,*}, Cyril Milleret¹, Pierre Dupont¹, Henrik Brøseth² &
7 Richard Bischof¹

8 1. Faculty of Environmental Sciences and Natural Resource Management, Norwegian

9 University of Life Sciences, P.O. Box 5003, 1432 Ås, Norway

10 2. Department of Terrestrial Ecology, Norwegian Institute for Nature Research, PB

11 5685 Torgarden, 7485 Trondheim, Norway

12 * Corresponding author – Email address: ehsan.moqanaki@gmail.com

13 <https://orcid.org/0000-0001-7968-0210>

14 Word count: 5820 (all inclusive)

15 Abstract

16 After centuries of intense persecution, several large carnivore species in Europe and
17 North America have experienced a rebound. Today's spatial configuration of large
18 carnivore populations has likely arisen from the interplay between their ecological traits
19 and current environmental conditions, but also from their history of persecution and
20 protection. Yet, due to the challenge of studying population-level phenomena, we
21 are rarely able to disentangle and quantify the influence of past and present factors
22 driving the spatial distribution and density of these controversial species. Using spatial
23 capture-recapture models and a data set of 742 genetically identified wolverines *Gulo*
24 *gulo* collected over $1/2$ million km² across their entire range in Norway and Sweden, we
25 identify landscape-level factors explaining the current population density of wolverines
26 in the Scandinavian Peninsula. Distance from the relic range along the Swedish-
27 Norwegian border, where the wolverine population survived a long history of persecution,
28 remains a key determinant of wolverine density today. However, regional differences in
29 management and environmental conditions also played an important role in shaping
30 spatial patterns in present-day wolverine density. Specifically, we found evidence of
31 slower recolonization in areas that had set lower wolverine population goals in terms
32 of the desired number of annual reproductions. Management of transboundary large
33 carnivore populations at biologically relevant scales may be inhibited by administrative
34 fragmentation. Yet, as our study shows, population-level monitoring is an achievable
35 prerequisite for a comprehensive understanding of the distribution and density of large
36 carnivores across an increasingly anthropogenic landscape.

37 **Keywords:** Abundance, Density, Distribution, Large carnivores, Non-invasive moni-
38 toring, Spatial capture-recapture, Transboundary wildlife, *Gulo gulo*

39 **1 Introduction**

40 Species distributions we observe today are the result of not only ecological traits and
41 current local environmental conditions, but also land-use history, human activity, and
42 management strategies ([Donohue et al. 2000](#), [Foster et al. 2003](#), [Di Marco and Santini](#)
43 [2015](#)). Emerging disturbance regimes, such as altered frequency and intensity of extreme
44 weather and climate events ([Ummenhofer and Meehl 2017](#)), further impact species
45 distributions. Identifying and disentangling the factors that lead to the distribution
46 and dynamics of species is one of the most profound and long-standing research areas
47 in ecology, with both fundamental and applied implications ([Guisan and Zimmermann](#)
48 [2000](#), [Elith and Leathwick 2009](#), [Jetz et al. 2019](#)).

49 Humans are the main transformers of Earth's ecosystems ([Ellis 2011](#), [Pereira et al.](#)
50 [2012](#), [Waters et al. 2016](#)), with a growing list of documented effects on wildlife ([Yackulic](#)
51 [et al. 2011](#), [Tucker et al. 2018](#)). Despite a broad overall consistency in wildlife responses
52 to anthropogenic disturbances, there is considerable variability in scale, magnitude, and
53 pattern of human impacts ([Tablado and Jenni 2017](#), [Gaynor et al. 2018](#), [Tucker et al.](#)
54 [2018](#)). A popular example is the case of large carnivore species that have undergone
55 substantial range contractions due to intensive persecution by humans. While many
56 species continue to struggle, some have in recent decades successfully recolonized part
57 of their historic range, particularly in Western Europe and North America ([Linnell](#)
58 [et al. 2001](#), [Zedrosser et al. 2011](#), [Chapron et al. 2014](#), [Ripple et al. 2014](#), [Ingeman](#)
59 [et al. 2022](#)). Limited understanding of factors shaping the spatial configuration of
60 carnivore populations poses a challenge to science and management, and the current
61 knowledge gaps may hinder predictions of future responses in the face of increasing
62 human pressure.

63 The fall and rise of wolverines *Gulo gulo* in Scandinavia is a prime example of recovery
64 of an iconic large carnivore following intense persecution and range contraction. The

65 wolverine was historically distributed throughout most of the Scandinavian Peninsula
66 ([Landa et al. 2000](#), [Flagstad et al. 2004](#)). During the twentieth century, intensive
67 persecution of the wolverine reduced its range and population size drastically. By 1970,
68 the population was functionally extinct in many areas with the exception of a narrow
69 strip in the alpine region along the border between Sweden and Norway ([Landa et al.](#)
70 [2000](#), [Flagstad et al. 2004](#); Fig. 1). The situation was similarly grim in neighboring
71 Finland, where wolverine observations were rare beyond the borderland with Russia
72 ([Lansink et al. 2020](#); Fig. 1). The wolverine finally received legal protection in both
73 Norway and Sweden by 1973, and later followed by Finland, and gradually recolonized
74 many parts of its historical range in Scandinavia ([Flagstad et al. 2004](#), [Aronsson and](#)
75 [Persson 2017](#), [Lansink et al. 2020](#)). Today, the wolverine population is established
76 across Norway and Sweden beyond the alpine refuge areas ([Chapron et al. 2014](#), [Gervasi](#)
77 [et al. 2016](#), [Bischof et al. 2020](#)). The return of the wolverine has rekindled conflict
78 with the sheep-farming industry and semi-domesticated reindeer *Rangifer tarandus*
79 husbandry ([Flagstad et al. 2004](#), [Hobbs et al. 2012](#), [Persson et al. 2015](#), [Aronsson and](#)
80 [Persson 2017](#)). The wolverine is listed on Appendix S2 of the Bern Convention for
81 both countries and is therefore formally “strictly protected”. However, because Norway
82 is not a member of the European Union, it is not bound by the same set of regulations.
83 Wolverines are therefore subject to persistent lethal control in Norway, while they are
84 strictly protected in Sweden under the European Union’s Habitats Directive 92/43
85 (annex IV; [Habitats Directive 1992](#)).

86 In a human-dominated world, understanding population-level drivers of species
87 spatial distribution and particularly density is important to understand and predict
88 the potential for species-environment interactions in a management context. What we
89 know about landscape and environmental factors influencing wolverine distribution
90 and density has been cobbled together from a small patchwork of studies, often with
91 limited spatial extent, in various parts of the global distribution range of the species
92 ([Fisher et al. 2022](#)). In Scandinavia, population and landscape-level determinants of

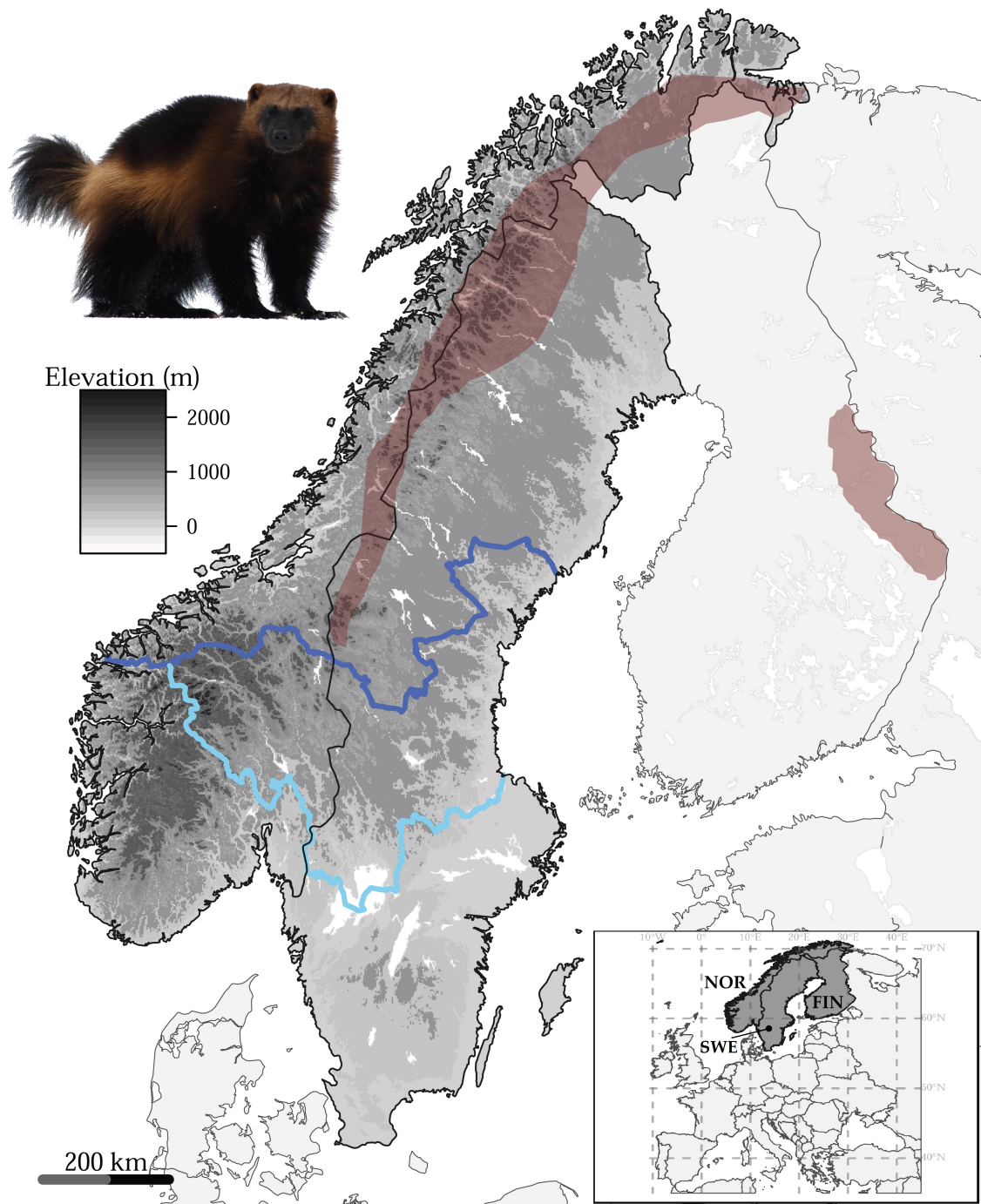


Figure 1: Approximate wolverine *Gulo gulo* distribution in Scandinavia (red polygon on the left) and Finland (red polygon on the right) in the 1970's, when the population range was at its lowest in modern times following intense human persecution (i.e., the relic range; redrawn after [Landa et al. \(2000\)](#) and [Chapron et al. \(2014\)](#)). Blue lines separate zones containing administrative units (i.e., large carnivore management regions in Norway and counties in Sweden) with shared population goals for the wolverine (see [Table 1](#)). We merged the zones below the dark blue line into one southern zone in each country. Photo credit: Karel Bartik/www.shutterstock.com

93 wolverine distribution and density are poorly known. Historical (Landa et al. 2000)
94 and current (Chapron et al. 2014) range maps suggest that recolonization in this
95 anthropogenic landscape has been facilitated by favorable legislation and improved
96 cultural acceptance (Linnell et al. 2001, Flagstad et al. 2004, Aronsson and Persson
97 2017). However, there is evidence that biophysical constraints, such as climate, habitat,
98 and terrain, have played a greater role in shaping the current spatial distribution
99 of the wolverine at the continental scale (Cretois et al. 2021). Current management
100 decisions use information that is largely based on data from the high-conflict alpine
101 areas (Brøseth et al. 2010, Aronsson and Persson 2017) but would benefit from a better
102 knowledge of the determinants of wolverine's spatial variation in density across its
103 entire Scandinavian range. Until recently, this was out of reach because of the rarity
104 and elusive behavior of the species, the vast geographic expanse of the population, and
105 spatially incomplete surveys (Flagstad et al. 2004, Gervasi et al. 2016, Aronsson and
106 Persson 2017).

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

120 **2 Methods**

121 **2.1 Non-invasive genetic sampling**

122 We used wolverine non-invasive genetic sampling (NGS) data from the Scandinavian
123 large carnivore monitoring database (Rovbase 3.0; www.rovbase.no and www.rovbase.se). This is one of the largest, long-term capture-recapture data of terrestrial wildlife
124 globally ([Bischof et al. 2020](#), [Tourani 2022](#)). Wildlife authorities and volunteers conduct
125 globally (Bischof et al. 2020, Tourani 2022). Wildlife authorities and volunteers conduct
126 both structured searches and opportunistic sampling of putative wolverine scats and
127 hair on snow between December and June each year throughout the species' range
128 in Norway and Sweden. The structured search tracks and locations of non-invasive
129 samples are GPS recorded (Fig. S1). Further details on wolverine NGS is provided
130 elsewhere (e.g., [Brøseth et al. 2010](#), [Gervasi et al. 2016](#), [Bischof et al. 2020](#)). Samples
131 were processed and analyzed by two dedicated DNA labs using a number of control
132 measures to minimize genotyping errors, as described elsewhere ([Ekblom et al. 2018](#),
133 [Flagstad et al. 2019](#), [Lansink et al. 2022](#)). First, samples were analyzed with a Single
134 Nucleotide Polymorphism (SNP)-chip with 96 markers and, second, all individuals were
135 analyzed with 19 microsatellite markers to determine species and identity of wolverine
136 individuals as well as their sex. We used NGS data collected between 1 December
137 2018 and 30 June 2019, which consisted of individual identity, sex, collection date, and
138 coordinates associated with each wolverine sample. This sampling period represents
139 the latest, most complete, semi-systematic wolverine NGS effort across the entire range
140 of the wolverine population in Scandinavia to date ([Flagstad et al. 2019](#), [Bischof et al.](#)
141 [2020](#), [Milleret et al. 2022](#)).

142 **2.2 Analysis**

143 SCR models offer a flexible framework to account for imperfect detection of indi-
144 viduals and provide spatially explicit estimates of abundance (i.e., density) and other
145 population parameters ([Efford 2004](#), [Borchers and Efford 2008](#), [Royle et al. 2014](#)). The

146 SCR modeling framework can support flexible sampling configurations and incorporate
147 both individual- and detector-level covariates to account for sources of heterogeneity
148 in detectability, and spatial covariates to account for variation in density (Royle et al.
149 2014). Although building spatially indexed hierarchical models, such as SCR, can
150 be computationally challenging or even prohibitive for large spatial extents, recent
151 developments have resulted in dramatic improvements (e.g., Milleret et al. 2019, Turek
152 et al. 2021, Zhang et al. 2022). Here, we build on these recent developments to study
153 the landscape-scale determinants of the Scandinavian wolverine density.

154 2.2.1 Spatial capture-recapture model

155 We built a single-season (i.e., demographically closed) SCR model in a Bayesian
156 framework by expanding on our previous work (Bischof et al. 2020). Our SCR model
157 contains two hierarchical levels: (1) The observation sub-model accounts for imperfect
158 and variable wolverine detectability during NGS; and (2) The ecological sub-model
159 describes wolverine density as the main ecological process of interest in this study. Our
160 SCR model estimates the following parameters: (1) the baseline detection probability
161 p_0 : detection probability at a trap or hypothetical detector located at an animal's
162 activity center s_i , a latent variable representing the expected location about which an
163 individual uses space during the sampling period; (2) the spatial scale parameter of
164 the detection function σ ; (3) the number N of wolverine activity centers within the
165 available habitat S (i.e., the detector grid and a buffer around it; see below), which
166 can be used to derive density D (see below); and (4) the effects (regression coefficient
167 β) of spatial and individual covariates on the detection probability and density.

168 **(1) The observation sub-model:** We used the conventional half-normal detection
169 function (Borchers and Efford 2008, Royle et al. 2014) to model the probability p of
170 detecting individual i at detector j as a decreasing function of the distance d between
171 the detector and the individual's center of activity s_i : $p_{ij} = p_{0_{ij}} \exp(-d_{ij}^2/2\sigma^2)$. The
172 detection function is assumed to reflect individual space use and is therefore directly

173 linked with the home range concept (Royle et al. 2014). Because we used a data-
174 augmentation approach (Royle et al. 2007), the detection of an individual has to be
175 made conditional on the individual's state z_i ($z_i = 1$ when individual i is member of the
176 population N), which is governed by the inclusion probability ψ : $z_i \sim \text{Bernoulli}(\psi)$.
177 The population size can be then derived by summing the z_i 's: $N = \sum_{i=1}^M z_i$, where M
178 is the chosen size of the data-augmented population (Royle et al. 2007) and represents
179 the maximum number of wolverines in the habitat S (see *Ecological sub-model*).

180 In our study, detectors are the centers of 5 572 10×10 km grid cells, covering a land
181 area extending 100 km beyond the outermost wolverine NGS detections collected during
182 the sampling period (Fig. S1). We used a partially aggregated binomial observation
183 model (Milleret et al. 2018) to retain more information from the wolverine NGS data by
184 dividing each main detector cell into 25 sub-detector cells of 2×2 km. By retrieving the
185 number of sub-detector cells with at least one non-invasive sample for each wolverine
186 detected at each main detector cell, we generated individual spatial detection histories
187 (Royle et al. 2014). Finally, we placed a 40-km buffer around the detector grid to define
188 the habitat S . This value was chosen based on the average home-range radius of adult
189 Scandinavian wolverines (Persson et al. 2010, Mattisson et al. 2011, Aronsson et al.
190 2022), so that the buffer is larger than three times the estimated σ of 10.3 km (95%
191 credible interval [CI] = 10.1 – 10.5 km) for male wolverines as reported by Bischof et al.
192 (2020). This buffer area allows detection of individuals even if their activity centers
193 are located outside the detector grid (Efford 2004, 2011). The detector grid covered
194 most of the contiguous Scandinavian Peninsula over Norway and Sweden ($58^\circ 08' - 70^\circ$
195 $42' N$, $5^\circ 56' - 32^\circ 46' E$; Fig. S1), while parts of the buffer (41.6%) fell inside Finland
196 and Russia. Thus, the available habitat was 633 200 km², after removing large lakes
197 and other non-contiguous land areas, of which 88% (557 200 km²) were in Norway and
198 Sweden (Fig. S1).

199 Wolverine NGS was conducted by hundreds of field staff and volunteers across

200 different jurisdictions in Norway and Sweden. We therefore expected spatial variability
201 in detection probability of wolverine individuals (Efford et al. 2013, Moqanaki et al.
202 2021). Following Bischof et al. (2020), we considered a different baseline detection
203 probability for each jurisdiction $p_{0_{County}}$ ($County = 1:8$) to account for possible regional
204 differences in monitoring regimes. Jurisdictions were defined based on carnivore
205 management regions in Norway and counties in Sweden after Bischof et al. (2020) with
206 slight modifications to match with our habitat extent (Fig. S2). We merged neighboring
207 jurisdictions to ensure sufficient wolverine detections for estimating baseline detection
208 probability in each unit (Bischof et al. 2020). In addition, we modeled the effect of
209 three detector- and one individual-level covariates that may influence the probability
210 of wolverine detection (Table S1):

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

211 \mathbf{Effort}_j is the length (m) of GPS search tracks within each detector grid cell j recorded
212 during the structured NGS, \mathbf{Road}_j is the logarithm of the average geographic distance
213 (km) from each detector to the nearest road of any type, and \mathbf{Snow}_j is the average
214 percentage of snow cover in each detector grid cell during the sampling months (De-
215 cember 2018 - June 2019; Table S1). We also modeled individual variation linked with
216 detection in the previous sampling year $\mathbf{Previous}_i$; a binary covariate which takes the
217 value 1 if individual i was detected in the previous sampling year and 0 otherwise.
218 During NGS, investigators are believed to have the tendency to prioritize searching
219 in locations where their searches were previously successful, which could positively
220 influence the detection probability of those previously-detected wolverine individuals
221 during the focal sampling year (Gervasi et al. 2014, Milleret et al. 2022). Availability
222 of the monitoring data from the previous year made it possible to account for this
223 potential source of heterogeneity in wolverine detectability. This individual binary
224 covariate $\mathbf{Previous}_i$ is latent for augmented individuals and was modeled following
225 a Bernoulli distribution: $\mathbf{Previous}_i \sim \text{Bernoulli}(\pi)$, where π is the probability that

226 an arbitrary individual from the population was detected in the previous year. All
227 continuous spatial covariates were scaled before SCR model fitting. Further details
228 on detection covariates, the rationale to include them, and their original source and
229 spatial depiction are provided in Table S1 and Figure S3.

230 **(2) The Ecological sub-model** describes the number and distribution of all
231 wolverines present in the population (i.e., detected and non-detected). We used a data
232 augmentation approach (Royle et al. 2007) to account for those wolverine individuals
233 that were not detected during NGS, where the super-population size M (i.e., detected
234 and augmented individuals) is chosen to be considerably larger than N . Following
235 Bischof et al. (2020) and given the relatively high detectability of the target population
236 during NGS (Milleret et al. 2022), we chose an augmentation factor of 0.8 to facilitate
237 the analysis by Markov chain Monte Carlo (MCMC). Thus, M was large enough such
238 that the probability that M individuals were alive in S during NGS was negligible.

239 SCR estimates of abundance are spatially explicit, meaning that they are derived
240 from the estimated location of all individual activity centers s_i with $z_i = 1$ across the
241 available habitat S (Efford 2004, Borchers and Efford 2008, Royle et al. 2014). The
242 collection of activity centers can be seen as the realization of a statistical point process
243 (Illian et al. 2008). To study how wolverine density varies in Scandinavia in response
244 to a number of environmental and history-related covariates (Table 1), we used an
245 inhomogeneous binomial point process to model spatial variation in the distribution of
246 individual activity centers with intensity function (Zhang et al. 2022): $\lambda(s) = e^{\beta \mathbf{X}(s)}$,
247 where $\mathbf{X}(s)$ is a vector of spatial covariate values evaluated at location s and β is a
248 vector of associated regression coefficients. The intensity function λ conditions the
249 placement of activity centers within each of the 20×20 km habitat grid cells s used
250 in this analysis (Fig. S1). In this formulation, no intercept is needed as the number
251 of activity centers is conditioned by data augmentation; thus, regression coefficients
252 represent the relative effects of the different covariates on wolverine density (Zhang

253 [et al. 2022](#)).

254 To disentangle the determinants of wolverine density within Scandinavia, we mea-
255 sured habitat characteristics at the scale of the home range of a wolverine (i.e., the
256 second order of habitat selection; [Johnson 1980](#)). We selected biotic and abiotic
257 covariates following previous studies on wolverine distribution and habitat use and
258 preferences ([Fisher et al. 2022](#) and references therein; Table 1). Specifically, we selected
259 covariates that may explain spatial variation in wolverine density in Scandinavia at
260 broad scale (Table 1; Fig. S4): (1) Distance from the relic range ([Landa et al. 2000](#),
261 [Flagstad et al. 2004](#); Fig. 1) to describe recolonization history; (2) Terrain Ruggedness
262 Index (TRI) explaining general topographic complexity; (3) Average percentage of
263 year-round snow cover as a measure of climate suitability (which was different from
264 the snow covariate used as a detector-level covariate; Table S1); (4) Percentage of
265 forest representing land use and habitat productivity; (5) Moose *Alces alces* harvest
266 density as a proxy for wild prey biomass availability, (6) Percentage of human set-
267 tlement areas as a measure of human disturbances, and (7) Zonal management to
268 account for regional differences in wolverine management plans and other environmental
269 conditions. The impact of current management was specifically included because of
270 unique management goals for wolverines in different areas of Norway and Sweden
271 ([Ministry of the Environment 2003](#), [Naturvårdsverket Ärendenr 2020](#)). Briefly, we
272 divided our habitat layer into northern and southern zones in each country ($n = 4$;
273 Fig. S4, Table 1) by aggregating jurisdictions with similar management goals for the
274 number of wolverine annual reproduction and other environmental conditions (e.g.,
275 climate, prey availability and abundance, and human influence). We simplified the
276 spatial variation in wolverine management by merging several counties or carnivore
277 management regions, and partially included jurisdictions in the southern part of each
278 country without management goals (Table 1; Fig. 1), since these southern counties
279 contained no NGS and wolverine detections in our data set (Fig. S1). Likewise, we
280 merged the buffer area in neighboring Finland and Russia with the northern zones

281 (Fig. S4). We then calculated the proportion overlap between each habitat cell and
282 the resulting four zones to define four spatial covariates (Fig. S4). Because the four
283 proportions sum to one, we did not use the first zone covariate to avoid identifiability
284 issues (i.e., the northern zone in Sweden, zone 1.a in Table 1, was an implicit intercept).
285 Since management goals and other zone-specific characteristics of the biotic and abiotic
286 environment may also have affected the wolverine’s ability to recolonize away from the
287 relic range, we included an interaction term between the distance from the relic range
288 and each of the four zones:

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

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

295 We transformed all covariate raster layers from the original projection to the
296 Universal Transverse Mercator (UTM zone 33N) and locally interpolated the raster
297 values using the “bilinear” method of the `resample` function of the R package `raster`
298 (Hijmans 2021) to match the 20×20 km habitat grid used in this analysis (Figs. S1
299 and S4). All continuous covariates were then standardized prior to their inclusion in
300 the model to have a mean of zero and one unit standard deviation. Further details
301 regarding the rationale for including each covariate, their sources, and their expected
302 effects are provided in Table 1 and Fig. S4.

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
Relic (\mathbf{X}_1)	Distance (m) from the relic range represents the founding population and colonization history. The relic 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 relic range area were assigned a value of 0. We then computed the Euclidean distance for all habitat cells to the nearest cell with a value of 0 using the <code>distance</code> function of the R package <code>raster</code> (Hijmans 2021).
Ruggedness (\mathbf{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, availability of cover, and level of human disturbances (May et al. 2008, 2012, Rauset et al. 2013, Poley et al. 2018)	+	Obtained through the <code>terrain</code> function of the R package <code>terra</code> (Hijmans et al. 2022) using an elevation layer (AWS Terrain Tiles and OT global datasets API) at about 256×256 m obtained via the <code>get_elev_raster</code> function of the R package <code>elevatr</code> (Hollister et al. 2021)
Snow (\mathbf{X}_3)	The average percentage of year-round snow cover across years 2008-2019, representing climate severity, denning suitability, and prey availability and catchability (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 500m Grid data set (www.neo.sci.gsfc.nasa.gov)
Forest (\mathbf{X}_4)	Percentage of forest 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 ESA-CCI Land Cover project (categories 50, 60, 61, 62, 70, 71, 72, 80; www.esa-landcover-cci.org) at about 176×176 m
Moose (\mathbf{X}_5)	An index of moose <i>Alces alces</i> density using hunting bags, representing habitat productivity and a proxy for wild prey biomass availability (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, and Ålgdata 2021b). We used data from the previous hunting season (Sep-Oct 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 <code>focal</code> function of the R package <code>raster</code> (Hijmans 2021)
Settlement (\mathbf{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 about 57-m resolution from the World Settlement Footprint data set (WSF2015; Marconcini et al. 2020) and log transformed after adding a value of 1 to deal with 0 values
Zonal management ($\mathbf{R}_1 \dots \mathbf{R}_4$)	An aggregation of administrative units (i.e., large carnivore management regions in Norway and counties in Sweden) with shared population goals for the wolverine ($n = 4$ zones; Ministry of the 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: (1.a) Norrbotten, Västerbotten, and Jämtland (Sweden) plus a small fraction of the buffer, and (1.b) Management region 8 (Finmark and Troms), region 7 (Nordland) and region 6 (Trøndelag and Møre og Romsdal) in Norway; (2) Southern zones with the management goal of less than 10 annual wolverine reproductions: (2.a) Västernorrland, Dalarna, Gävleborg, and Värmland plus a small part of the neighboring counties with no management goals: Västmanland, Västra Götaland, and Örebro (Sweden), and (2.b) Management region 5 (Hedmark) and region 3 (Oppland) plus a small part of the neighboring counties with no management goals: Sogn og Fjordane, Hordaland, Rogaland, Vest-Agder, Aust-Agder, Telemark, Buskerud, and Vestfold (Norway)

303 2.2.2 Implementation

304 We fitted SCR models with NIMBLE (version 0.12.2; [de Valpine et al. 2022](#)) in R
305 (version 4.2.1; [R Core Team 2022](#)) for female and male wolverines separately using
306 the recent developments by [Turek et al. \(2021\)](#) and custom functions made available
307 through the R package `nimbleSCR` ([Bischof et al. 2021](#)). We ran four MCMC chains,
308 each with 200 000 iterations, discarded the initial 10 000 samples as burn-in, and
309 thinned by a factor of 10. We assessed mixing of chains by inspecting traceplots, and
310 we considered models as converged when the potential scale reduction value (\hat{R}) was
311 ≤ 1.10 for all parameters ([Brooks and Gelman 1998](#)). Data and R code for fitting the
312 SCR model are provided in the Supplementary Information, and Table S2 shows the
313 list of priors used.

314 To explore the relative importance of each covariate on density, we incorporated
315 a Bayesian variable selection approach in NIMBLE using reversible jump MCMC with
316 indicator variables ([Green 1995](#), [O’Hara and Sillanpää 2009](#)). We incorporated an
317 indicator variable w associated with each regression coefficient β ($n = 12$; Table S2).
318 Thus, we modified equation (2) to include ($w = 1$) or exclude ($w = 0$) the effect of
319 each coefficient in the presence of other covariate effects in a given posterior draw:
320 $\lambda(s) = e^{\beta_1 w_1 \mathbf{X}_1(s) + \dots + \beta_p w_p \mathbf{X}_p(s)}$. We constrained inclusion of the interaction coefficients
321 to when the corresponding main effects were also included. For inference on the different
322 coefficients, we discarded MCMC draws where $w = 0$.

323 We calculated the median and the 95% CI limits of the posterior distribution for
324 all parameters, except for abundance, where we reported mean and 95% CI. To obtain
325 total wolverine abundance, we combined N estimates of male and female wolverines by
326 merging posterior MCMC samples from the sex-specific SCR models. In both total
327 and sex-specific models, we summed the total number of predicted activity center
328 locations of alive individuals ($z_i = 1$) within each habitat cell for each iteration of the

329 MCMC chains; thus, we generated a cell-based posterior distribution of abundance
330 that can be viewed also as density. Using this approach, we extracted abundance and
331 density estimates and the associated uncertainty for different spatial units relevant for
332 wolverine management at the country level, besides the total estimates for the entire
333 population in Scandinavia.

334 We constructed two types of sex-specific density maps: (1) a realized density
335 map based on the posterior location of activity centers as described above, and
336 (2) an expected density map based on the estimated intensity of the density point
337 process per habitat cell of 20×20 km and the estimate of population size: $\mathbf{D}_{\text{exp}}(s) =$
338 $N\lambda(s)/\sum_{h=1}^S \lambda(h)$. “Realized” density maps show density based on the average model-
339 estimated activity center locations of individuals, as opposed to “expected” density
340 maps, which show predicted density based on the regression model underlying the
341 intensity surface. To present uncertainty, we calculated and mapped the standard
342 deviation of the per-cell posterior of density (Miller et al. 2013).

343 **3 Results**

344 **3.1 Non-invasive genetic sampling**

345 During the sampling period between 1 December 2018 and 30 June 2019, 283 282 km
346 of GPS search tracks were recorded within our designated detector grid (Fig. S1) across
347 Norway (34%) and Sweden (66%). The final NGS data set consisted of 2 444 (1 350 male
348 and 1 094 female) detections from 742 (335 males and 407 females) genetically identified
349 wolverine individuals across the entire population on the Scandinavian Peninsula (Fig.
350 S1). The number of detections (i.e., recaptures) per identified individual ranged from 1
351 to 13 for both sexes (mean = 3.0 males and 2.1 females).

3.2 Density predictors

The variation in wolverine density across Scandinavia was explained by distance from the relic range in different zones, percentage of human settlements, moose harvest density, year-round snow, terrain ruggedness, and percentage of forest (Fig. 2). The magnitude of the effects and uncertainty around them varied moderately between the sexes (Figs. S5 and 2). For both females and males, the effects of being in southern Norway, distance from the relic range in northern Sweden, and percentage of human settlements received the most support based on the inclusion probability (≥ 0.99 ; Figs. 2 and S5). In addition, for female wolverines the effects of being in northern Norway and distance from the relic range in southern Norway, and for males the effect of moose harvest density received inclusion probabilities of ≥ 0.99 (Figs. 2 and S5).

Among the covariates considered, percentage of human settlements had the largest negative effects on both female and male wolverine densities (median and 95% CI β_{X_5} = -1.61, -2.66 to -0.79 [female] and -2.27, -3.41 to -1.33 [male]; Figs. S5 and 2). Likewise, distance from the relic range negatively affected the density of both sexes, with significantly stronger effects in southern Norway ($\beta_{R_4X_1}$ = -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 relic range in northern Sweden (Figs. S5 and 3). Based on our results, we predicted that areas located 30 km away from the relic range, as-the-crow-flies, would have on average about two-third lower expected wolverine densities in the southern zones of Norway and Sweden compared to the northern zones (Fig. 3). Moose harvest density was positively associated with both female and male wolverine densities (β_{X_6} = 0.19, 0.02 to 0.35 [female] and 0.46, 0.31 to 0.63 [male]; Figs. S5 and 2). The effects of percentage of forest (β_{X_4} = 0.32, 0.12 to 0.52) and terrain ruggedness on density was significantly positive for female wolverines only (β_{X_2} = 0.42, 0.25 to 0.59), while the effect of year-round snow cover was positive for males only (β_{X_3} = 0.35, 0.11 to 0.56; Fig. S5; Table S3).

379 **3.3 Detection predictors**

380 The effects of detection covariates varied slightly between male and female wolverines
381 (Table S3). Baseline detection probability p_0 was comparable between sexes (median
382 and 95% CI $p_0 = 0.02$, 0.01 to 0.02 for both males and females), but varied moderately
383 among the eight carnivore management regions and counties in Norway and Sweden
384 (Fig. S2). Both female and male wolverine detection probabilities increased with
385 search effort ($\beta_E = 0.62$, 0.53 to 0.71 [female] and 0.51, 0.44 to 0.59 [male]). Further,
386 for female wolverines, searching farther away from the nearest road increased their
387 detectability ($\beta_R = 0.19$, 0.07 to 0.31). Higher percentage of snow cover during the
388 sampling months decreased detectability of males ($\beta_S = -0.22$, -0.37 to -0.08). The
389 individual-level covariate representing wolverine detection in the previous sampling
390 year positively influenced male wolverine detectability only ($\beta_P = 0.61$, 0.44 to 0.77),
391 suggesting sex-specific detection bias during NGS. The spatial scale parameter was
392 greater for males ($\sigma_m = 8$ km, 7.6 - 8.2) than for females ($\sigma_f = 6$ km, 5.6 - 6.4). More
393 details are provided in the Supplementary Material.

394 **3.4 Sex-specific and total estimates of abundance and density**

395 We estimated the abundance of the Scandinavian wolverine population within our
396 detector grid (Fig. S1) during the 2018/2019 sampling period at 408 (95% CI = 397 -
397 420) males and 667 (95% CI = 640 - 697) females. The wolverine population in Sweden
398 was estimated to be between 640 and 692 individuals, while in Norway we estimated
399 between 397 and 425 wolverines (Fig S6). Overall, we predicted higher wolverine
400 densities for both males and females closer to the relic range, but the pattern was more
401 pronounced for females (Fig. 4).

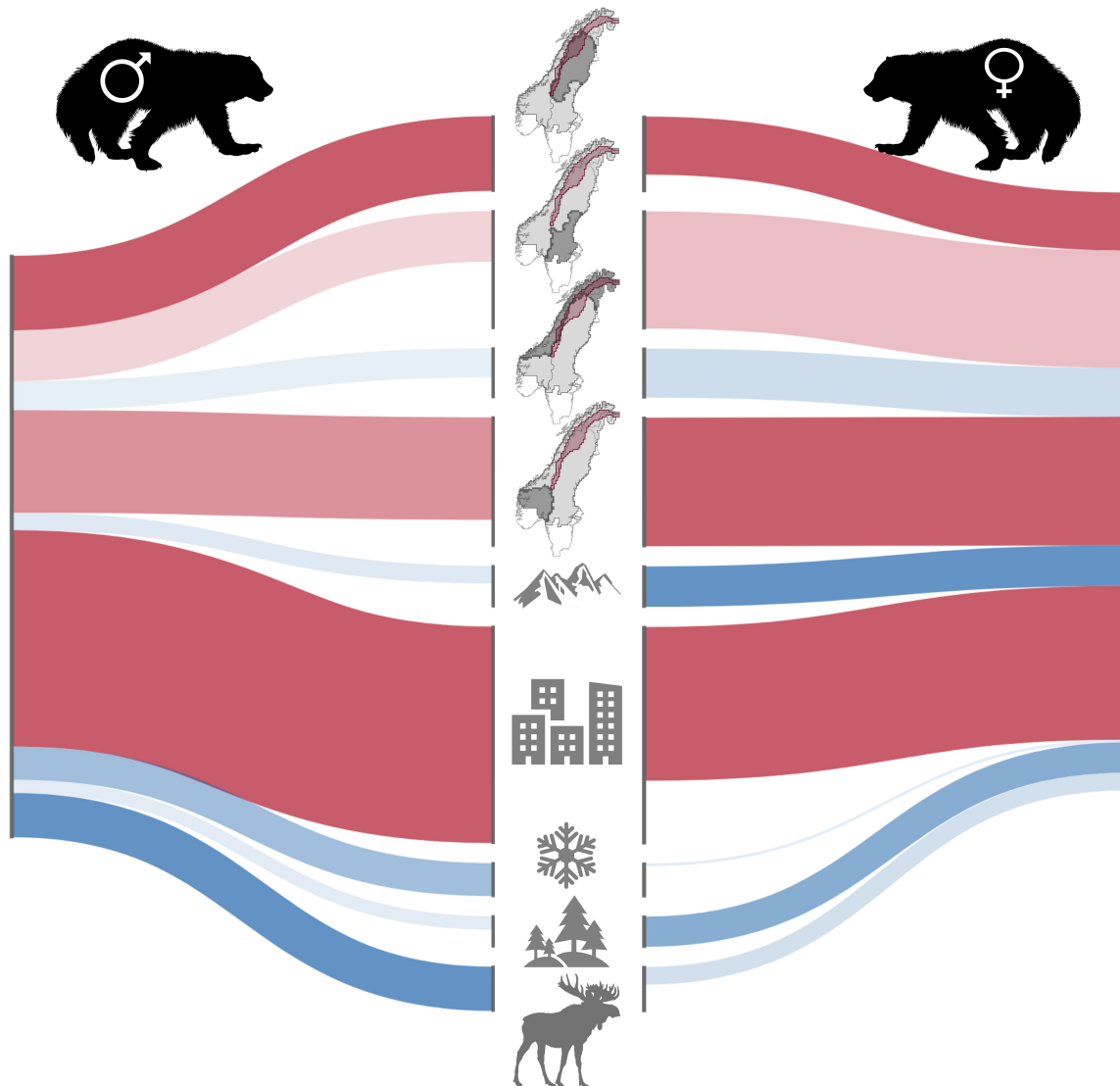


Figure 2: The effect of environmental covariates (middle column) on density of male (left) and female (right) wolverines *Gulo gulo* in Scandinavia between December 2018 and June 2019 as estimated by sex-specific spatial capture-recapture models. Line width represents the magnitude of the median effect (i.e., the thicker, the larger the strength of the covariate effects). Line color shows direction of the effects (blue = positive and red = negative effects), and the opacity level indicates the amount of support for the inclusion of each covariate in the model (inclusion probability of 0 [transparent] to 1 [opaque]). For interaction effects of distance from the relic range in different zones (top four), the line width indicates differences of coefficient estimates from the zone in northern Sweden (the top line). The density covariates are (from top to bottom): Distance from the relic range in (1) northern Sweden, (2) southern Sweden, (3) northern Norway, and (4) southern Norway; (5) Terrain Ruggedness Index; (6) percentage of human settlements; (7) the average percentage of year-round snow cover; (8) percentage of forest; and (9) moose *Alces alces* harvest density (Table 1). The main additive effects of zones are not shown (see Fig. S5).

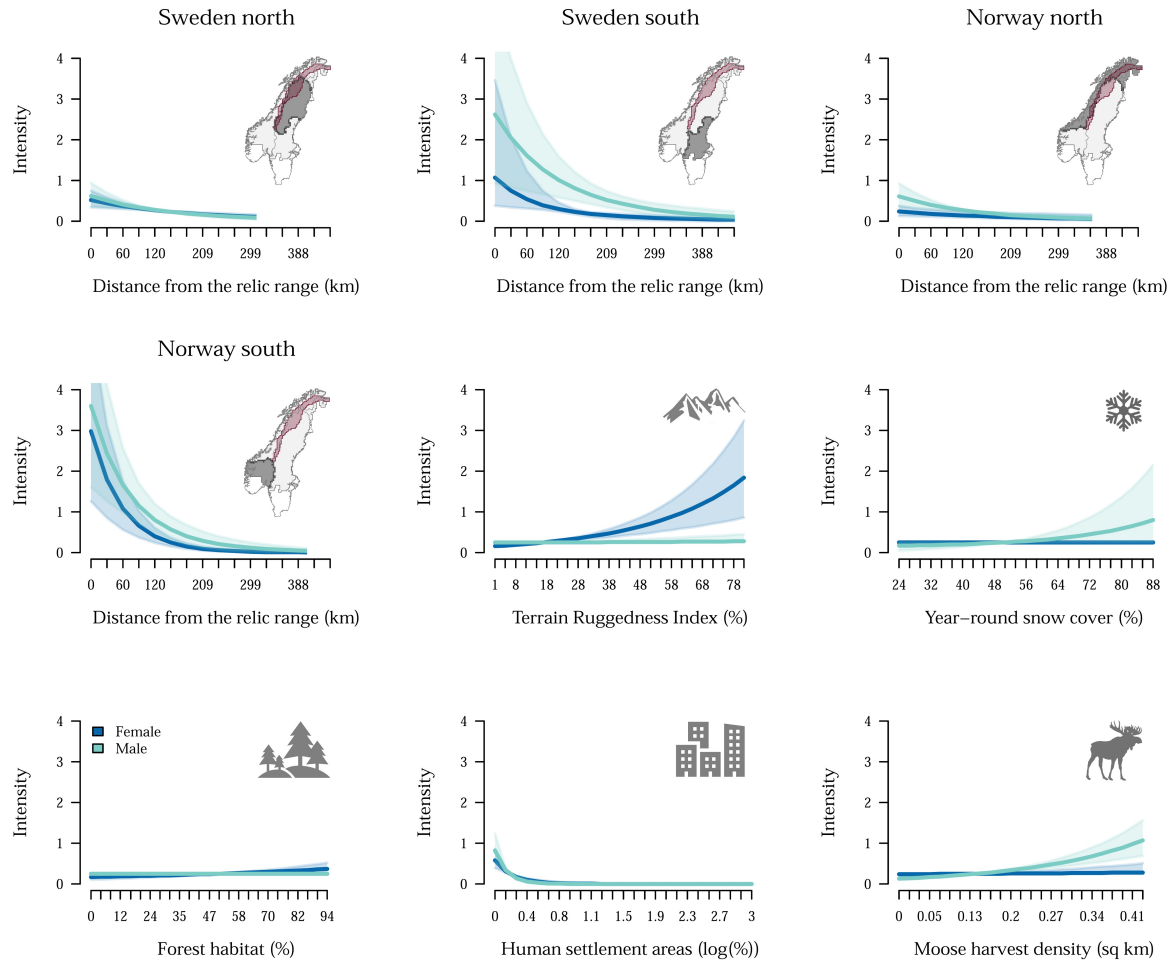


Figure 3: Expected intensity of the density point process for female (blue) and male (green) wolverines *Gulo gulo* in Scandinavia as a function of environmental covariates. Mean response and 95% credible interval are represented by thick lines and transparent polygons, respectively. Predictions in the first four plots from top-left are for the range of values of distance from the relic range (km) that were available in the given zone. The red polygons on the small maps indicate the relic 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 (Fig. S4).

402 4 Discussion

403 The present spatial configuration of wolverine density across Scandinavia reflects
 404 the species' recovery from past range-contraction and population decline, modulated by
 405 current management goals and environmental conditions. The importance of the relic
 406 range along the Swedish-Norwegian border highlights the need for coordinated moni-

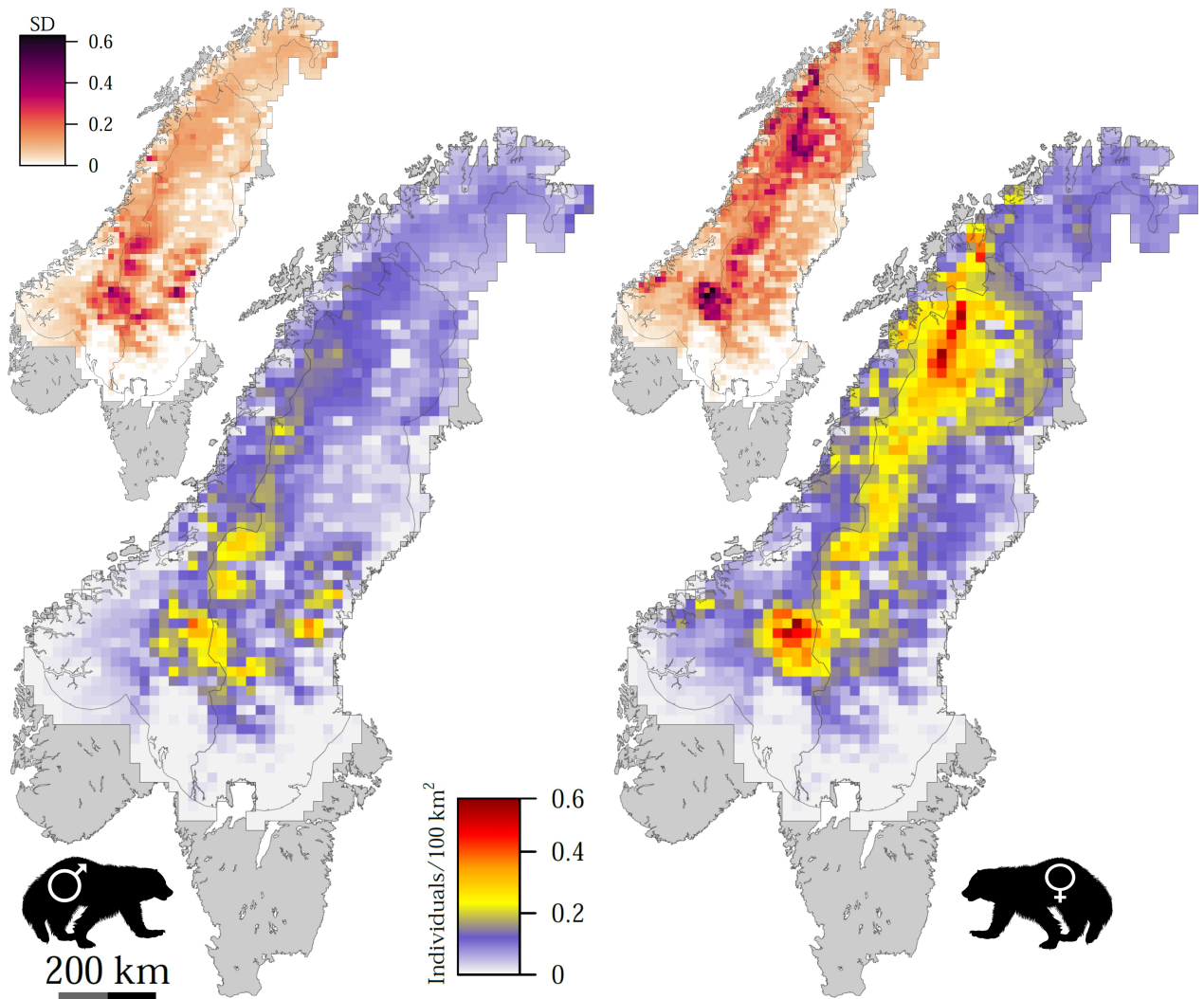


Figure 4: Expected density surfaces of male (left) and female (right) wolverines *Gulo gulo* in Scandinavia as a function of environmental covariates included in spatial capture-recapture analysis (Table 1). The main maps show the average expected density surfaces for each sex (wolverines/100 km²) and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

407 toring and management of this transboundary population of wolverines. Monitoring is
408 already coordinated to some extent ([Gervasi et al. 2016](#), [Aronsson and Persson 2017](#),
409 [Bischof et al. 2020](#)), but fully coordinated management is made difficult by existing
410 differences in national and regional population goals and legal obligations.

411 **The ghosts of the past**

412 A key driver of current wolverine density distribution for both sexes in Scandinavia
413 appears to be distance from the relic range (Figs. 1 and S4), where Scandinavian
414 wolverines survived human persecution before their legal protection in the 1970's
415 ([Landa et al. 2000](#), [Flagstad et al. 2004](#)). We also found that zonal management is
416 one of the main drivers of wolverine density in Scandinavia (Figs. 3 and S5). The
417 density of both male and female wolverines declines with increasing distance from
418 the relic range, and the rate of decline further varies among zones with contrasting
419 management goals regarding wolverine annual reproduction (Figs. 2-3). Regional
420 differences in the effect of distance from the relic range is likely a sign that the
421 current recolonization of wolverines is both a function of past and current management
422 practices and environmental conditions. Together, these factors explained much of the
423 spatial variation in current density of wolverines in the Scandinavian Peninsula (Fig.
424 4). Whether the relic range represents highly suitable habitat for the Scandinavian
425 wolverine (i.e., historical and current core) or the species was pushed into the alpine
426 refuge areas during the peak of the persecution is not fully understood ([Landa et al.](#)
427 [2000](#), [Flagstad et al. 2004](#), [Kerley et al. 2012](#), [Zigouris et al. 2013](#)). Nonetheless,
428 wolverine recolonization in Scandinavia matches the general pattern of return of other
429 large carnivore species in Western Europe and North America ([Linnell et al. 2001](#),
430 [Chapron et al. 2014](#)). Successful recovery of these species is partially attributed to
431 changing public attitudes towards large carnivores and effective law enforcement, which,
432 in turn have lowered the risk of direct killing by humans ([Zedrosser et al. 2011](#), [Chapron](#)
433 [et al. 2014](#), [Ingeman et al. 2022](#)). Likewise, increasing tolerance towards wolverines by

434 Scandinavian farmers and traditional pastoralists has in part been achieved through
435 intensive zonal management of wolverines and compensation schemes ([Persson et al.](#)
436 [2015](#), [Aronsson and Persson 2017](#)). Balancing the landscape-level requirements of a
437 viable wolverine (meta-)population and human interests will therefore remain crucial
438 for the successful management.

439 The ability of wolverines to travel long distances has probably contributed to their
440 successful recolonization in part of their historical range in Scandinavia. However,
441 male wolverines are more likely to disperse, while females usually stay close to their
442 natal range and show high home-range fidelity ([Inman et al. 2012](#), [Packila et al. 2017](#),
443 [Aronsson and Persson 2018](#), [Aronsson et al. 2022](#)). We found that spatial covariates
444 tested in our study had qualitatively similar effects on the density of female and male
445 wolverines (Figs. 2 and S5). We note that male and female Scandinavian wolverines
446 have a comparable level of culling mortality ([Bischof et al. 2020](#)). Additionally, long-
447 distance dispersal events that lead to successful colonization of unoccupied habitat are
448 not common ([Flagstad et al. 2004](#), [Packila et al. 2017](#)). Even if male wolverines on
449 average disperse farther, they may not always successfully establish significantly farther
450 than females. Nonetheless, we observed pockets of higher expected male wolverine
451 density farther from the relic range compared to the expected female density which
452 remained the highest in and near the relic range (Fig. 4). This pattern was reflected in
453 the sex-specific estimates of coefficient for the additive effects of distance from the relic
454 range in the southern zones of Sweden and Norway (Fig. S5).

455 We estimated, on average, substantially lower wolverine densities in the southern
456 zones of Norway and Sweden compared to the northern zones (Fig. 3). The southern
457 zones generally do not cover semi-domesticated reindeer husbandry areas and calving
458 grounds, but include areas with free-ranging domestic sheep, especially in Norway.
459 The current management strategy in both countries allows more wolverine annual
460 reproduction in the northern zones ([Ministry of the Environment 2003](#), [Naturvårdsverket](#)

461 [Ärendén 2020](#)), and the legal removal of wolverines is proportionally more intense in the
462 south to protect the free-ranging sheep ([Strand et al. 2019](#)). There are also mismatches
463 between the management goals, their implementation, and regional tolerance of the
464 wolverine in Scandinavia ([Aronsson and Persson 2017](#)) that are not entirely reflected by
465 the four zones we considered. Thus, it is likely that the combined effect of the higher
466 cost of dispersal from the relic range and the current management plans regarding
467 wolverine recolonization, together with region-specific environmental characteristics,
468 have resulted in slower wolverine expansion and lower densities in the southern parts
469 of the Scandinavian Peninsula.

470 **Population-level drivers of variation in density**

471 Wildlife distributions and densities are continuously being shaped by multiple
472 factors at different spatio-temporal scales. Abiotic factors, such as temperature and
473 precipitation, play a key role in shaping species distributions at broad scales ([Benton
474 2009](#)). There is also increasing evidence that biotic factors are important determinants
475 of species distributions at both local and large spatial extents, particularly when
476 accounting for interacting drivers ([Van der Putten et al. 2010](#), [Wisz et al. 2013](#)).
477 We found that current environmental features that describe landscape heterogeneity
478 and productivity can explain variation in the Scandinavian wolverine density at the
479 landscape level. Although the relative importance of some of these covariates varied
480 between sexes (Figs. 2 and S5), anthropogenic factors had a consistently negative impact
481 on both male and female wolverine density. Besides quantifying the driving factors of
482 density for the entire population of the Scandinavian wolverines, our study advances
483 the previous findings ([Fisher et al. 2022](#) and references in Table 1) by highlighting
484 the role of past persecution history and current management practices in modulating
485 natural recolonization across a human-dominated landscape.

486 Human-caused mortality and anthropogenic fragmentation of habitat are limiting

487 wolverine distribution and density globally (May et al. 2006, Persson et al. 2009,
488 Mowat et al. 2020, Lukacs et al. 2020, Lansink et al. 2022, Barrieto et al. 2022).
489 Within the Scandinavian large carnivore guild, wolverines are believed to be the most
490 sensitive to habitat fragmentation (May et al. 2008). We included the percentage of
491 human settlement areas as a measure of human pressure on the natural environment
492 (Marconcini et al. 2020), which represents human population density and the associated
493 disturbances. The negative impact of human settlements on wolverine density appeared
494 to be substantial (Figs. 2 and S5), and we observed drastic declines in the expected
495 density of both male and female wolverines with increasing human settlements (Fig. 3).
496 In Norway and Sweden, the majority of large towns with the highest concentration of
497 permanent human settlements and high traffic-volume roads are located in the southern
498 parts. Likewise, the farthest distance from the relic range and zones with lower annual
499 wolverine reproduction goals are also in the south (Figs. 3 and S4). Thus, the combined
500 effect of all these anthropogenic factors have probably limited the wolverine density
501 distribution in the southern parts of the Scandinavian Peninsula. Nonetheless, the
502 south represents the wolverine population's expansion front and the observed latitudinal
503 pattern may be also explained with the observation that wildlife population dynamics
504 can differ considerably from the core areas (Swenson et al. 1998, Burton et al. 2010,
505 Angert et al. 2020). With increasing human-made barriers to wolverine movement and
506 dispersal (Aronsson and Persson 2018, Sawaya et al. 2019, Lansink et al. 2022), we
507 expect the resulting population fragmentation will also play a major role in shaping
508 the spatial distribution and dynamics of the Scandinavian wolverine population in the
509 future.

510 As a measure of wild prey biomass availability, we included moose harvest density in
511 our models (Table 1, Fig. S4). We estimated significantly higher wolverine densities in
512 areas with higher moose harvest density, and this positive effect was more pronounced
513 for males (Fig. 3). Wolverines are generally facultative scavengers and in many areas
514 of Fennoscandia, they depend on slaughter remains from hunting and carcasses of prey

515 killed by other top predators, including the Eurasian lynx *Lynx lynx*, wolf *Canis lupus*,
516 and brown bear *Ursus arctos*, as well as animals dead from natural causes and roadkills
517 (Van Dijk et al. 2008, Mattisson et al. 2011, Koskela et al. 2013, Aronsson et al. 2022).
518 Moose occurs throughout the wolverine range in Scandinavia and moose carrion is an
519 important food source for wolverines in many areas (Van Dijk et al. 2008, Mattisson
520 et al. 2016, Aronsson et al. 2022), especially for breeding females (Koskela et al. 2013)
521 and during winter (October - April) that overlaps with our study period. There is,
522 however, considerable spatial and temporal variation in wolverine diet in Scandinavia,
523 with reindeer as the most important prey for wolverines in some areas (Mattisson et al.
524 2016). Unfortunately, we were unable to find comprehensive and reliable data on the
525 density of wild or semi-domesticated reindeer across the entire Scandinavian Peninsula
526 to be considered for our study.

527 The positive effects of terrain ruggedness and the percentage of forest on wolverine
528 density were significant for females only, while the average percentage of year-round snow
529 appeared to only impact male density (Figs. 2 and S5). Traditionally, Scandinavian
530 wolverines are not considered to be a forest-dwelling species, as they appear to select
531 open and rugged terrain at higher elevations with snow, away from human activity (May
532 et al. 2008, 2012, Rauset et al. 2013). Spring snow cover in particular is believed to be
533 important for reproducing females as it determines denning suitability and offspring
534 survival (Copeland et al. 2010, Mowat et al. 2020, Barrueto et al. 2022). However, in
535 recent years, the Scandinavian wolverine population has expanded considerably into
536 the boreal forest and has now colonized areas without persistent spring snow cover
537 (Aronsson and Persson 2017). We chose the average year-round snow cover during the
538 past decade not to specifically account for denning suitability for the wolverine, but as
539 a measure of climatic niche suitability that may have shaped the wolverine's density
540 distribution today (Table 1). Terrain ruggedness and forest cover probably correlate
541 with the degree of past persecution due to accessibility and history of land protection
542 (Joppa and Pfaff 2009, Kerley et al. 2012) and the significance of these covariates for

543 female wolverines may then reflect their affinity for high-quality habitat compared to
544 males ([May et al. 2008, 2012](#), [Rauset et al. 2013](#), [Aronsson and Persson 2018](#)).

545 **Wolverines in the past, present, and future**

546 Scandinavian wolverines have recovered from the brink of extinction and are now
547 occupying a considerable portion of their historic range ([Flagstad et al. 2004](#), [Chapron
548 et al. 2014](#), [Gervasi et al. 2016](#), [Aronsson and Persson 2017](#), [Bischof et al. 2020](#)). The
549 effects of past impacts are nonetheless still clearly visible today, modulated, but not
550 masked, by current environmental conditions and management regimes. The wolverine
551 density in Scandinavia is shaped by human interests, while interacting with the history
552 of local extinction. Wolverines are also impacted by other environmental covariates,
553 several of which are directly or indirectly influenced by humans (e.g., prey base, climate
554 conditions, and land-use). In an increasingly human-dominated landscape, the impact
555 of humans on wolverines is likely to be even greater in the coming decades, further
556 defining the state of the Scandinavian wolverine population. Despite the expansion of
557 wolverines ([Chapron et al. 2014](#), [Aronsson and Persson 2017](#)), an increasing human
558 impact, if neglected, may therefore eventually again limit wolverines to the relic range
559 that served as a refuge in the past.

560 **Data Availability Statement**

561 Wolverine detections used in this study are available through the database Rovbase
562 3.0 at www.rovbase.no or www.rovbase.se. Data and R scripts of the spatial capture-
563 recapture analysis will be deposited upon acceptance at: [https://github.com/
564 eMoqanaki](https://github.com/eMoqanaki).

565 **Authors' contributions**

566 R.B. and E.M. conceived and designed the study; H.B. provided the wolverine
567 data and context on wolverine monitoring and management in Scandinavia; E.M.

568 implemented the analysis with contributions from C.M., R.B., P.D., and H.B.; E.M.
569 wrote the first draft and all co-authors discussed and contributed to the manuscript;
570 all authors gave final approval for publication.

571 **Competing interests**

572 We declare we have no interests which might be perceived as posing a conflict or
573 bias.

574 **Funding**

575 This study was funded by the Norwegian Environment Agency (Miljødirektoratet),
576 the Swedish Environmental Protection Agency (Naturvårdsverket), and the Research
577 Council of Norway through the project WildMap (NFR 286886). E.M. was supported
578 by a PhD scholarship from the Norwegian University of Life Sciences awarded to R.B.

579 **Acknowledgments**

580 We thank all contributors to the Scandinavian large carnivore monitoring database
581 Rovbase 3.0. M. Tourani helped with the implementation of the variable selection
582 approach and provided feedback on the figures. J. Kindberg provided access to the
583 moose harvest data used in this study. S. Dey and S. Schowanek commented on an
584 earlier version of the manuscript.

585 **References**

586 A. L. Angert, M. G. Bontrager, and J. Ågren. What do we really know about adaptation
587 at range edges? *Annual Review of Ecology, Evolution, and Systematics*, 51:341–361,
588 2020.

589 M. Aronsson and J. Persson. Mismatch between goals and the scale of actions constrains
590 adaptive carnivore management: the case of the wolverine in sweden. *Animal*

591 *Conservation*, 20(3):261–269, 2017.

592 M. Aronsson and J. Persson. Female breeding dispersal in wolverines, a solitary
593 carnivore with high territorial fidelity. *European Journal of Wildlife Research*, 64(1):
594 1–10, 2018.

595 M. Aronsson, J. Persson, B. Zimmermann, J. Märtz, P. Wabakken, R. Heeres, and
596 K. Nordli. *Järven i Inre Skandnaviens skogslandskap–områdesbruk, födoval och*
597 *reproduktion*. SLU Grimsö forskningsstation Institutionen för ekologi Sveriges lant-
598 bruksuniversitet, 2022.

599 M. Barrueto, M. A. Sawaya, and A. P. Clevenger. Low wolverine (*Gulo gulo*) density
600 in a national park complex of the Canadian Rocky Mountains. *Canadian Journal of*
601 *Zoology*, 98(5):287–298, 2020.

602 M. Barrueto, A. Forshner, J. Whittington, A. P. Clevenger, and M. Musiani. Protection
603 status, human disturbance, snow cover and trapping drive density of a declining
604 wolverine population in the [canadian rocky mountains]. *Scientific Reports*, 12(1):
605 1–15, 2022.

606 M. J. Benton. The red queen and the court jester: species diversity and the role of
607 biotic and abiotic factors through time. *Science*, 323(5915):728–732, 2009.

608 R. Bischof, C. Milleret, P. Dupont, J. Chipperfield, M. Tourani, A. Ordiz, P. de Valpine,
609 D. Turek, J. A. Royle, O. Gimenez, et al. Estimating and forecasting spatial
610 population dynamics of apex predators using transnational genetic monitoring.
611 *Proceedings of the National Academy of Sciences*, 117(48):30531–30538, 2020.

612 R. Bischof, D. Turek, C. Milleret, T. Ergon, P. Dupont, S. Dey, W. Zhang, and
613 P. de Valpine. *nimbleSCR: Spatial Capture-Recapture (SCR) Methods Using ‘nimble’*,
614 2021.

615 D. L. Borchers and M. G. Efford. Spatially explicit maximum likelihood methods for
616 capture-recapture studies. *Biometrics*, 64(2):377–385, 2008.

- 617 S. P. Brooks and A. Gelman. General methods for monitoring convergence of iterative
618 simulations. *Journal of Computational and Graphical Statistics*, 7(4):434–455, 1998.
- 619 H. Brøseth, Ø. Flagstad, C. Wårdig, M. Johansson, and H. Ellegren. Large-scale
620 noninvasive genetic monitoring of wolverines using scats reveals density dependent
621 adult survival. *Biological Conservation*, 143(1):113–120, 2010.
- 622 O. J. Burton, B. L. Phillips, and J. M. Travis. Trade-offs and the evolution of
623 life-histories during range expansion. *Ecology Letters*, 13(10):1210–1220, 2010.
- 624 G. Chapron, P. Kaczensky, J. D. Linnell, M. Von Arx, D. Huber, H. Andrén, J. V.
625 López-Bao, M. Adamec, F. Álvares, O. Anders, et al. Recovery of large carnivores in
626 europe’s modern human-dominated landscapes. *Science*, 346(6216):1517–1519, 2014.
- 627 M. Cimatti, N. Ranc, A. Benítez-López, L. Maiorano, L. Boitani, F. Cagnacci,
628 M. Čengić, P. Ciucci, M. A. Huijbregts, M. Krofel, et al. Large carnivore ex-
629 pansion in Europe is associated with human population density and land cover
630 changes. *Diversity and Distributions*, 27(4):602–617, 2021.
- 631 J. Copeland, K. McKelvey, K. Aubry, A. Landa, J. Persson, R. Inman, J. Krebs,
632 E. Lofroth, H. Golden, J. Squires, et al. The bioclimatic envelope of the wolverine
633 (*Gulo gulo*): do climatic constraints limit its geographic distribution? *Canadian*
634 *Journal of Zoology*, 88(3):233–246, 2010.
- 635 B. Cretois, J. D. Linnell, B. Van Moorter, P. Kaczensky, E. B. Nilsen, J. Parada,
636 and J. K. Rød. Coexistence of large mammals and humans is possible in europe’s
637 anthropogenic landscapes. *iScience*, 24(9):103083, 2021.
- 638 P. de Valpine, C. Paciorek, D. Turek, N. Michaud, C. Anderson-Bergman, F. Obermeyer,
639 C. Wehrhahn Cortes, A. Rodríguez, D. Temple Lang, and P. S. *NIMBLE User*
640 *Manual*, 2022. URL <https://r-nimble.org>. R package manual version 0.12.2.
- 641 M. Di Marco and L. Santini. Human pressures predict species’ geographic range size
642 better than biological traits. *Global Change Biology*, 21(6):2169–2178, 2015.

- 643 K. Donohue, D. R. Foster, and G. Motzkin. Effects of the past and the present on
644 species distribution: land-use history and demography of wintergreen. *Journal of*
645 *Ecology*, 88(2):303–316, 2000.
- 646 M. Efford. Density estimation in live-trapping studies. *Oikos*, 106(3):598–610, 2004.
- 647 M. G. Efford. Estimation of population density by spatially explicit capture–recapture
648 analysis of data from area searches. *Ecology*, 92(12):2202–2207, 2011.
- 649 M. G. Efford, D. L. Borchers, and G. Mowat. Varying effort in capture-recapture
650 studies. *Methods in Ecology and Evolution*, 4(7):629–636, 2013.
- 651 R. Ekblom, B. Brechlin, J. Persson, L. Smeds, M. Johansson, J. Magnusson, Ø. Flagstad,
652 and H. Ellegren. Genome sequencing and conservation genomics in the Scandinavian
653 wolverine population. *Conservation Biology*, 32(6):1301–1312, 2018.
- 654 J. Elith and J. R. Leathwick. Species distribution models: ecological explanation
655 and prediction across space and time. *Annual Review of Ecology, Evolution, and*
656 *Systematics*, 40:677–697, 2009.
- 657 E. C. Ellis. Anthropogenic transformation of the terrestrial biosphere. *Philosophical*
658 *Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*,
659 369(1938):1010–1035, 2011.
- 660 J. T. Fisher, S. Murray, M. Barrueto, K. Carroll, A. P. Clevenger, D. Hausleitner,
661 W. Harrower, N. Heim, K. Heinemeyer, A. L. Jacob, et al. Wolverines (*Gulo gulo*) in a
662 changing landscape and warming climate: A decadal synthesis of global conservation
663 ecology research. *Global Ecology and Conservation*, page e02019, 2022.
- 664 Ø. Flagstad, E. Hedmark, A. Landa, H. Brøseth, J. Persson, R. Andersen, P. Segerström,
665 and H. Ellegren. Colonization history and noninvasive monitoring of a reestablished
666 wolverine population. *Conservation Biology*, 18(3):676–688, 2004.

- 667 Ø. Flagstad, O. Kleven, S. E. Erlandsen, H. Brandsegg, M. H. Spets, M. H. Spets, L. B.
668 Eriksen, I. P. Ø. Andersskog, M. Johansson, R. Ekblom, H. Ellegren, and H. Brøseth.
669 DNA-based monitoring of the Scandinavian wolverine population 2019: Nina report
670 1762. Technical report, Norwegian Institute for Nature Research (NINA), 2019. URL
671 <http://hdl.handle.net/11250/263426>.
- 672 D. Foster, F. Swanson, J. Aber, I. Burke, N. Brokaw, D. Tilman, and A. Knapp. The
673 importance of land-use legacies to ecology and conservation. *BioScience*, 53(1):77–88,
674 2003.
- 675 K. M. Gaynor, C. E. Hojnowski, N. H. Carter, and J. S. Brashares. The influence of
676 human disturbance on wildlife nocturnality. *Science*, 360(6394):1232–1235, 2018.
- 677 V. Gervasi, H. Brøseth, O. Gimenez, E. B. Nilsen, and J. D. Linnell. The risks of
678 learning: confounding detection and demographic trend when using count-based
679 indices for population monitoring. *Ecology and Evolution*, 4(24):4637–4648, 2014.
- 680 V. Gervasi, H. Brøseth, O. Gimenez, E. B. Nilsen, J. Odden, Ø. Flagstad, and J. D.
681 Linnell. Sharing data improves monitoring of trans-boundary populations: the case
682 of wolverines in central scandinavia. *Wildlife Biology*, 22(3):95–106, 2016.
- 683 P. J. Green. Reversible jump markov chain monte carlo computation and bayesian
684 model determination. *Biometrika*, 82(4):711–732, 1995.
- 685 A. Guisan and N. E. Zimmermann. Predictive habitat distribution models in ecology.
686 *Ecological Modelling*, 135(2-3):147–186, 2000.
- 687 Habitats Directive. Council directive 92/43/eec of 21 may 1992 on the conservation of
688 natural habitats and of wild fauna and flora. *Official Journal of the European Union*,
689 206:7–50, 1992.
- 690 R. J. Hijmans. *raster: Geographic Data Analysis and Modeling*, 2021. URL <https://CRAN.R-project.org/package=raster>. R package version 3.4-13.
691

692 R. J. Hijmans, R. Bivand, J. van Etten, K. Forner, J. Ooms, and E. Pebesma. *Package*
693 *'terra': Spatial Data Analysis*, 2022. URL [https://CRAN.R-project.org/package=](https://CRAN.R-project.org/package=terra)
694 [terra](#). R package version 1.5-21.

695 N. T. Hobbs, H. Andren, J. Persson, M. Aronsson, and G. Chapron. Native predators
696 reduce harvest of reindeer by Sámi pastoralists. *Ecological Applications*, 22(5):
697 1640–1654, 2012.

698 J. Hollister, T. Shah, A. L. Robitaille, M. W. Beck, and M. Johnson. *elevatr: Access*
699 *Elevation Data from Various APIs*, 2021. URL [https://github.com/jhollist/](https://github.com/jhollist/elevatr/)
700 [elevatr/](#). R package version 0.4.1.

701 J. Illian, A. Penttinen, H. Stoyan, and D. Stoyan. *Statistical analysis and modelling of*
702 *spatial point patterns*, volume 70. John Wiley & Sons, 2008.

703 K. E. Ingeman, L. Z. Zhao, C. Wolf, D. R. Williams, A. L. Ritger, W. J. Ripple, K. L.
704 Kopecky, E. M. Dillon, B. P. DiFiore, J. S. Curtis, et al. Glimmers of hope in large
705 carnivore recoveries. *Scientific Reports*, 12(1):1–13, 2022.

706 R. M. Inman, M. L. Packila, K. H. Inman, A. J. Mccue, G. C. White, J. Persson, B. C.
707 Aber, M. L. Orme, K. L. Alt, S. L. Cain, et al. Spatial ecology of wolverines at
708 the southern periphery of distribution. *The Journal of Wildlife Management*, 76(4):
709 778–792, 2012.

710 N. J. Isaac, M. A. Jarzyna, P. Keil, L. I. Dambly, P. H. Boersch-Supan, E. Browning,
711 S. N. Freeman, N. Golding, G. Guillera-Arroita, P. A. Henrys, et al. Data integration
712 for large-scale models of species distributions. *Trends in Ecology & Evolution*, 35(1):
713 56–67, 2020.

714 W. Jetz, M. A. McGeoch, R. Guralnick, S. Ferrier, J. Beck, M. J. Costello, M. Fernandez,
715 G. N. Geller, P. Keil, C. Merow, et al. Essential biodiversity variables for mapping
716 and monitoring species populations. *Nature Ecology & Evolution*, 3(4):539–551, 2019.

- 717 D. H. Johnson. The comparison of usage and availability measurements for evaluating
718 resource preference. *Ecology*, 61(1):65–71, 1980.
- 719 L. N. Joppa and A. Pfaff. High and far: biases in the location of protected areas. *PLoS*
720 *ONE*, 4(12):e8273, 2009.
- 721 G. I. Kerley, R. Kowalczyk, and J. P. Crooms. Conservation implications of the
722 refugee species concept and the European bison: king of the forest or refugee in a
723 marginal habitat? *Ecography*, 35(6):519–529, 2012.
- 724 A. Kortello, D. Hausleitner, and G. Mowat. Mechanisms influencing the winter
725 distribution of wolverine *Gulo gulo luscus* in the southern Columbia Mountains,
726 Canada. *Wildlife Biology*, 2019(1):1–13, 2019.
- 727 A. Koskela, J. Aspi, M. Hyvärinen, et al. Effect of reproductive status on the diet
728 composition of wolverines (*Gulo gulo*) in boreal forests of eastern Finland. In *Annales*
729 *Zoologici Fennici*, volume 50, pages 100–106. BioOne, 2013.
- 730 A. Landa, M. Lindén, I. Kojola, et al. *Action plan for the conservation of wolverines*
731 *in Europe (Gulo gulo)*. Number 18-115. Council of Europe, 2000.
- 732 G. Lansink, O. Kleven, R. Ekblom, G. Spong, A. Kopatz, J. Mattisson, J. Persson,
733 I. Kojola, K. Holmala, T. Ollila, et al. Potential for increased connectivity between
734 differentiated wolverine populations. *Biological Conservation*, 272:109601, 2022.
- 735 G. M. Lansink, R. Esparza-Salas, M. Joensuu, A. Koskela, D. Bujnáková, O. Kleven,
736 Ø. Flagstad, T. Ollila, I. Kojola, J. Aspi, et al. Population genetics of the wolverine
737 in Finland: the road to recovery? *Conservation Genetics*, 21(3):481–499, 2020.
- 738 J. D. Linnell, J. E. Swenson, and R. Anderson. Predators and people: conservation
739 of large carnivores is possible at high human densities if management policy is
740 favourable. *Animal Conservation*, 4(4):345–349, 2001.

- 741 P. M. Lukacs, D. Evans Mack, R. Inman, J. A. Gude, J. S. Ivan, R. P. Lanka, J. C.
742 Lewis, R. A. Long, R. Sallabanks, Z. Walker, et al. Wolverine occupancy, spatial
743 distribution, and monitoring design. *The Journal of Wildlife Management*, 84(5):
744 841–851, 2020.
- 745 M. Marconcini, A. Metz-Marconcini, S. Üreyen, D. Palacios-Lopez, W. Hanke, F. Ba-
746 chofer, J. Zeidler, T. Esch, N. Gorelick, A. Kakarla, et al. Outlining where humans
747 live, the world settlement footprint 2015. *Scientific Data*, 7(1):1–14, 2020.
- 748 J. Mattisson, J. Persson, H. Andren, and P. Segerström. Temporal and spatial
749 interactions between an obligate predator, the Eurasian lynx (*Lynx lynx*), and a
750 facultative scavenger, the wolverine (*Gulo gulo*). *Canadian Journal of Zoology*, 89
751 (2):79–89, 2011.
- 752 J. Mattisson, G. R. Rauset, J. Odden, H. Andrén, J. D. Linnell, and J. Persson.
753 Predation or scavenging? prey body condition influences decision-making in a
754 facultative predator, the wolverine. *Ecosphere*, 7(8):e01407, 2016.
- 755 R. May, A. Landa, J. van Dijk, J. D. Linnell, and R. Andersen. Impact of infrastructure
756 on habitat selection of wolverines *Gulo gulo*. *Wildlife Biology*, 12(3):285–295, 2006.
- 757 R. May, J. Van Dijk, P. Wabakken, J. E. Swenson, J. D. Linnell, B. Zimmermann,
758 J. Odden, H. C. Pedersen, R. Andersen, and A. Landa. Habitat differentiation
759 within the large-carnivore community of Norway’s multiple-use landscapes. *Journal*
760 *of Applied Ecology*, 45(5):1382–1391, 2008.
- 761 R. May, L. Gorini, J. Van Dijk, H. Brøseth, J. Linnell, and A. Landa. Habitat charac-
762 teristics associated with wolverine den sites in Norwegian multiple-use landscapes.
763 *Journal of Zoology*, 287(3):195–204, 2012.
- 764 D. L. Miller, M. L. Burt, E. A. Rexstad, and L. Thomas. Spatial models for distance
765 sampling data: recent developments and future directions. *Methods in Ecology and*
766 *Evolution*, 4(11):1001–1010, 2013.

767 C. Milleret, P. Dupont, H. Brøseth, J. Kindberg, J. A. Royle, and R. Bischof. Using
768 partial aggregation in spatial capture recapture. *Methods in Ecology and Evolution*,
769 9(8):1896–1907, 2018.

770 C. Milleret, P. Dupont, C. Bonenfant, H. Brøseth, Ø. Flagstad, C. Sutherland, and
771 R. Bischof. A local evaluation of the individual state-space to scale up Bayesian
772 spatial capture–recapture. *Ecology and Evolution*, 9(1):352–363, 2019.

773 C. Milleret, P. Dupont, H. Brøseth, Ø. Flagstad, J. Kindberg, and R. Bischof. *Estimates*
774 *of wolverine density, abundance, and population dynamics in Scandinavia, 2013–2021*.
775 The Faculty of Environmental Sciences and Natural Resource Management (MINA),
776 Norwegian University of Life Sciences, 2022.

777 Ministry of the Environment. Rovvilt i norsk natur [Carnivores in Norwegian nature].
778 *Stortingsmelding 15 (2003–2004)*, 2003.

779 E. M. Moqanaki, C. Milleret, M. Tourani, P. Dupont, and R. Bischof. Consequences
780 of ignoring variable and spatially autocorrelated detection probability in spatial
781 capture-recapture. *Landscape Ecology*, 36(10):2879–2895, 2021.

782 A. T. Morehouse and M. S. Boyce. Grizzly bears without borders: Spatially explicit
783 capture–recapture in southwestern Alberta. *The Journal of Wildlife Management*,
784 80(7):1152–1166, 2016.

785 G. Mowat, A. P. Clevenger, A. D. Kortello, D. Hausleitner, M. Barrueto, L. Smit,
786 C. Lamb, B. DorsEy, and P. K. Ott. The sustainability of wolverine trapping
787 mortality in southern Canada. *The Journal of Wildlife Management*, 84(2):213–226,
788 2020.

789 Naturvårdsverket Ärendenr. Fastställande av minimivåer för järv gällande rovdjurs-
790 förvaltningsområden och län. *NV-01525-18*, 2020.

791 R. B. O’Hara and M. J. Sillanpää. A review of bayesian variable selection methods:
792 what, how and which. *Bayesian Analysis*, 4(1):85–117, 2009.

793 M. L. Packila, M. D. Riley, R. S. Spence, and R. M. Inman. Long-distance wolverine
794 dispersal from Wyoming to historic range in Colorado. *Northwest Science*, 91(4):
795 399–407, 2017.

796 H. M. Pereira, L. M. Navarro, and I. S. Martins. Global biodiversity change: the bad,
797 the good, and the unknown. *Annual Review of Environment and Resources*, 37:25–50,
798 2012.

799 J. Persson, G. Ericsson, and P. Segerström. Human caused mortality in the endangered
800 Scandinavian wolverine population. *Biological Conservation*, 142(2):325–331, 2009.

801 J. Persson, P. Wedholm, and P. Segerström. Space use and territoriality of wolverines
802 (*Gulo gulo*) in northern Scandinavia. *European Journal of Wildlife Research*, 56(1):
803 49–57, 2010.

804 J. Persson, G. R. Rauset, and G. Chapron. Paying for an endangered predator leads
805 to population recovery. *Conservation Letters*, 8(5):345–350, 2015.

806 L. G. Poley, A. J. Magoun, M. D. Robards, and R. L. Klimstra. Distribution and
807 occupancy of wolverines on tundra, northwestern Alaska. *The Journal of Wildlife*
808 *Management*, 82(5):991–1002, 2018.

809 R Core Team. *R: A Language and Environment for Statistical Computing*. R Foundation
810 for Statistical Computing, Vienna, Austria, 2022. URL [https://www.R-project.](https://www.R-project.org/)
811 [org/](https://www.R-project.org/).

812 G. R. Rauset, J. Mattisson, H. Andrén, G. Chapron, and J. Persson. When species'
813 ranges meet: assessing differences in habitat selection between sympatric large
814 carnivores. *Oecologia*, 172(3):701–711, 2013.

815 W. J. Ripple, J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite,
816 J. Berger, B. Elmhagen, M. Letnic, M. P. Nelson, et al. Status and ecological effects
817 of the world's largest carnivores. *Science*, 343(6167):1241484, 2014.

818 J. A. Royle, R. M. Dorazio, and W. A. Link. Analysis of multinomial models with
819 unknown index using data augmentation. *Journal of Computational and Graphical*
820 *Statistics*, 16(1):67–85, 2007.

821 J. A. Royle, R. B. Chandler, R. Sollmann, and B. Gardner. *Spatial Capture-Recapture*.
822 Academic Press, Waltham, 2014.

823 M. A. Sawaya, A. P. Clevenger, and M. K. Schwartz. Demographic fragmentation
824 of a protected wolverine population bisected by a major transportation corridor.
825 *Biological Conservation*, 236:616–625, 2019.

826 M. A. Scrafford, T. Avgar, B. Abercrombie, J. Tigner, and M. S. Boyce. Wolverine
827 habitat selection in response to anthropogenic disturbance in the western Canadian
828 boreal forest. *Forest Ecology and Management*, 395:27–36, 2017.

829 statistisk sentralbyrå. Moose hunting, 2021. URL [https://www.ssb.no/en/
830 jord-skog-jakt-og-fiskeri/jakt/statistikk/elgjakt](https://www.ssb.no/en/jord-skog-jakt-og-fiskeri/jakt/statistikk/elgjakt). Accessed: 2021-11-04.

831 G.-H. Strand, I. Hansen, A. de Boon, and C. Sandström. Carnivore management zones
832 and their impact on sheep farming in Norway. *Environmental Management*, 64(5):
833 537–552, 2019.

834 J. E. Swenson, F. Sandegren, and A. SO-Derberg. Geographic expansion of an increasing
835 brown bear population: evidence for presaturation dispersal. *Journal of Animal*
836 *Ecology*, 67(5):819–826, 1998.

837 Z. Tablado and L. Jenni. Determinants of uncertainty in wildlife responses to human
838 disturbance. *Biological Reviews*, 92(1):216–233, 2017.

839 M. Tourani. A review of spatial capture–recapture: Ecological insights, limitations,
840 and prospects. *Ecology and Evolution*, 12(1):e8468, 2022.

841 M. A. Tucker, K. Böhning-Gaese, W. F. Fagan, J. M. Fryxell, B. Van Moorter, S. C.
842 Alberts, A. H. Ali, A. M. Allen, N. Attias, T. Avgar, et al. Moving in the anthropocene:

843 Global reductions in terrestrial mammalian movements. *Science*, 359(6374):466–469,
844 2018.

845 D. Turek, C. Milleret, T. Ergon, H. Brøseth, P. Dupont, R. Bischof, and P. De Valpine.
846 Efficient estimation of large-scale spatial capture–recapture models. *Ecosphere*, 12
847 (2):e03385, 2021.

848 M. Ueno, E. J. Solberg, H. Iijima, C. M. Rolandsen, and L. E. Gangsei. Performance of
849 hunting statistics as spatiotemporal density indices of moose (*Alces alces*) in norway.
850 *Ecosphere*, 5(2):1–20, 2014.

851 C. C. Ummenhofer and G. A. Meehl. Extreme weather and climate events with
852 ecological relevance: a review. *Philosophical Transactions of the Royal Society B:
853 Biological Sciences*, 372(1723):20160135, 2017.

854 R. van de Schoot, S. Depaoli, R. King, B. Kramer, K. Märten, M. G. Tadesse,
855 M. Vannucci, A. Gelman, D. Veen, J. Willemsen, et al. Bayesian statistics and
856 modelling. *Nature Reviews Methods Primers*, 1(1):1–26, 2021.

857 W. H. Van der Putten, M. Macel, and M. E. Visser. Predicting species distribution
858 and abundance responses to climate change: why it is essential to include biotic
859 interactions across trophic levels. *Philosophical Transactions of the Royal Society B:
860 Biological Sciences*, 365(1549):2025–2034, 2010.

861 B. van der Veen, J. Mattisson, B. Zimmermann, J. Odden, and J. Persson. Refrigera-
862 tion or anti-theft? food-caching behavior of wolverines (*gulo gulo*) in scandinavia.
863 *Behavioral Ecology and Sociobiology*, 74(5):1–13, 2020.

864 J. Van Dijk, L. Gustavsen, A. Mysterud, R. May, Ø. Flagstad, H. Brøseth, R. Andersen,
865 R. Andersen, H. Steen, and A. Landa. Diet shift of a facultative scavenger, the
866 wolverine, following recolonization of wolves. *Journal of Animal Ecology*, 77(6):
867 1183–1190, 2008.

868 C. N. Waters, J. Zalasiewicz, C. Summerhayes, A. D. Barnosky, C. Poirier, A. Gałuszka,
869 A. Cearreta, M. Edgeworth, E. C. Ellis, M. Ellis, et al. The anthropocene is
870 functionally and stratigraphically distinct from the holocene. *Science*, 351(6269):
871 aad2622, 2016.

872 M. F. Wilson, B. O’Connell, C. Brown, J. C. Guinan, and A. J. Grehan. Multiscale
873 terrain analysis of multibeam bathymetry data for habitat mapping on the continental
874 slope. *Marine Geodesy*, 30(1-2):3–35, 2007.

875 M. S. Wisz, J. Pottier, W. D. Kissling, L. Pellissier, J. Lenoir, C. F. Damgaard, C. F.
876 Dormann, M. C. Forchhammer, J.-A. Grytnes, A. Guisan, et al. The role of biotic
877 interactions in shaping distributions and realised assemblages of species: implications
878 for species distribution modelling. *Biological Reviews*, 88(1):15–30, 2013.

879 C. B. Yackulic, E. W. Sanderson, and M. Uriarte. Anthropogenic and environmental
880 drivers of modern range loss in large mammals. *Proceedings of the National Academy
881 of Sciences*, 108(10):4024–4029, 2011.

882 A. Zedrosser, S. M. Steyaert, H. Gossow, and J. E. Swenson. Brown bear conservation
883 and the ghost of persecution past. *Biological Conservation*, 144(9):2163–2170, 2011.

884 W. Zhang, J. D. Chipperfield, J. B. Illian, P. Dupont, C. Milleret, P. de Valpine, and
885 R. Bischof. A flexible and efficient Bayesian implementation of point process models
886 for spatial capture-recapture data. *Ecology*, 2022.

887 J. Zigouris, J. A. Schaefer, C. Fortin, and C. J. Kyle. Phylogeography and post-glacial
888 recolonization in wolverines (*Gulo gulo*) from across their circumpolar distribution.
889 *PLoS ONE*, 8(12):e83837, 2013.

890 Älgdata. Statistik för älgdata, 2021a. URL [https://algdata-apps.lansstyrelsen.
891 se/algdata-apps-stat/](https://algdata-apps.lansstyrelsen.se/algdata-apps-stat/). Accessed: 2021-11-04.

892 L. Älgdata. Länsstyrelsernas karttjänst för beslutade älgförvaltningsområden och älgjak-

893 tsområden, 2021b. URL <https://ext-geoportal.lansstyrelsen.se/standard/>
894 [?appid=fc467ac65f7b4ddb435187e17aa33f](https://ext-geoportal.lansstyrelsen.se/standard/?appid=fc467ac65f7b4ddb435187e17aa33f). Accessed: 2021-11-04.