

Scale And Landscape Heterogeneity Influence The Predictive Performance of Habitat Suitability Models

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1 **Scale and landscape heterogeneity influence the predictive performance of habitat**
2 **suitability models**

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32 and Wildlife Management, WWF Sweden, and the Marie-Claire Cronstedts foundation.

33

34 **Context**

35 Resource selection functions (RSF) are used to predict habitat selection in a wide range of taxa for various
36 conservation and management purposes. Although such predictions often cover large geographic areas, the
37 limitations of extrapolating beyond the original study region are rarely addressed.

38

39 **Objectives**

40 Our first research objective was to demonstrate the implications of extrapolating RSF predictions across
41 different habitats and at different spatial scales, with regard to varying landscape characteristics. For our
42 second objective, we investigated the impact of individual variation in resource selection.

43

44 **Methods**

45 We used a long-term dataset of GPS-collared lynx from two separate regions in Sweden. We built individual-
46 level RSF models at two spatial scales for two different study regions to quantify individual and regional
47 variation in habitat selection, and extrapolated the results from each region across the opposing study area.

48

49 **Results**

50 Individual lynx selected resources differently within and between study regions, and predictions were more
51 accurate within home ranges than between home ranges. When extrapolating across variable landscapes,
52 encountering resource values outside the fitted range of the models led to incorrect predictions.

53

54 **Conclusions**

55 Our case study highlights the importance of quantifying a variable's value range in both the model and
56 extrapolation area, taking into account variation in individual resource selection, and understanding the
57 relationship with the order of selection to improve the reliability of habitat predictions. To increase the
58 transferability of models, extrapolations should ideally be limited to areas with overlapping value ranges, to
59 reduce the risk of misidentifying habitat suitability.

60

61

62 **Keywords (4 to 6 words):**

63 Resource Selection Function – Individual variation – Spatial scale – Habitat suitability – Habitat prediction –

64 Orders of Selection

65 **Introduction**

66 Habitat suitability models are common tools that use information on landscape attributes at species presence
67 locations to assess suitable habitat for a wide range of taxa (Cianfrani et al. 2010; Marini et al. 2010; Heinänen
68 et al. 2012; Guisan et al. 2013). These analyses are used for a variety of research and management purposes,
69 including to estimate the impact of changing landscape characteristics on the availability of suitable habitat for
70 a single species (Roscioni et al. 2014; Mikoláš et al. 2017), to compare the range and habitat overlap of
71 different species (Boyce 2006; Vergara et al. 2016), and to assess the historic range of a species (Hendricks et
72 al. 2016). Habitat suitability models can be applied at various scales, from an entire species' range (Viña et al.
73 2010; Yang et al. 2017), e.g. to predict range shifts under changing climate conditions (Marini et al. 2010; Hof
74 et al. 2012; Lyu and Sun 2014; Garden et al. 2015; Luo et al. 2015), to the individual level when predicting
75 the establishment of expanding populations of e.g. invasive species (Broennimann and Guisan 2008; Gormley
76 et al. 2011) or recolonizing native species (Inman et al. 2013; Bleyhl et al. 2015; D'Elia et al. 2015; Bateman
77 et al. 2016; Eriksson and Dalerum 2018).

78 Resource Selection Functions (RSFs) are a widely used type of habitat suitability models, which predict
79 suitable habitat by comparing resources at known locations of the study species with the overall availability of
80 certain environmental characteristics in the surrounding landscape (Boyce et al. 2002; Manly et al. 2007).

81 Decisions regarding species conservation and management based on RSF models are prevalent (Cianfrani et
82 al. 2010; Marini et al. 2010; Viña et al. 2010; DeCesare et al. 2012; Heinänen et al. 2012; Guisan et al. 2013;
83 Lyu and Sun 2014; Hodder et al. 2014; Garden et al. 2015; Luo et al. 2015; Yang et al. 2017). Often, when
84 predicting species' reestablishment and reintroduction as well as prospective shifts in a species' range, these
85 habitat predictions are extrapolated to include areas outside the monitored individuals', or the species' current
86 range (Falcucci et al. 2013; Inman et al. 2013; Bleyhl et al. 2015; Bateman 2016; Eriksson and Dalerum
87 2018).

88 Specific landscape characteristics and resource availability may differ between regions where a species
89 occurs, potentially reducing the reliability and transferability of predictions, where results are obtained using
90 data from a subset of a larger population (Boyce 2006; Guisan et al. 2013). Furthermore, differences in
91 selection between regions can occur because species may select resources differently under varying

92 environmental conditions or may be more behaviorally adapted to certain conditions than expected (Cianfrani
93 et al. 2010). Individuals within a species may also select resources differently, and individual variation is
94 increasingly recognized as an important factor affecting resource selection and could further evoke differences
95 in predictions (Gillingham and Parker 2008; Tinker et al. 2012; Leclerc et al. 2016; Ladle et al 2019).
96 Moreover, RSFs are scale-dependent, meaning that the ability of a certain variable in explaining habitat
97 selection and use may vary depending on the spatial scale of the analysis (Johnson 1980; Rettie and Messier
98 2000; Boyce 2006; Northrup et al. 2013).

99 Despite the aforementioned issues considering varying environmental characteristics, regional differences
100 in resource selection, and spatial scale, it is common to use data from a limited geographic area to predict
101 habitat selection for a much larger geographic area, due to limitations in data availability (Kuemmerle et al.
102 2011; Falcucci et al. 2013; Inman et al. 2013; Bleyhl et al. 2015; D’Elia et al. 2015; Bateman et al. 2016;
103 Eriksson and Dalerum 2018). When covering large geographic areas, we are confronted with landscapes
104 consisting of environmental characteristics which may differ significantly from those in the source area of the
105 species occurrence data (Kuemmerle et al. 2011; Inman et al. 2013; D’Elia et al. 2015; Bateman et al. 2016;
106 Eriksson and Dalerum 2018). In extreme cases, environmental predictors used in the original models are even
107 unavailable in the area to predict (e.g. D’Elia et al. 2015), thereby reducing the transferability of the habitat
108 suitability model. Such issues should be acknowledged and addressed (see D’Elia et al. 2015; Wan et al.
109 2019), since conservation efforts may be less effective if predictions misidentify habitat quality, which can
110 have severe implications when, for example, planning species reintroductions or establishing protected areas
111 aimed to promote species recovery.

112 As in many European countries, the Eurasian lynx (*Lynx lynx*) population in Scandinavia was nearly
113 eradicated in the early 20th century due to human persecution (Linnell et al. 2010; Chapron et al. 2014).
114 However, lynx were protected in 1928, and in 2018 the lynx population in Sweden was estimated to about
115 1000 – 1400 individuals (Tovmo and Zetterberg 2018). Since the beginning of the 21st century, lynx have
116 recolonized almost all of Sweden (Hemmingmoore et al. 2020), thereby inhabiting habitats with vastly
117 different environmental characteristics (Fig. 1a) (Rauset et al. 2013; Hemmingmoore et al. 2020). Due to their
118 occurrence across a wide environmental gradient, the lynx population in Sweden provides an ideal case study

119 in which we can assess the reliability and transferability of habitat predictions using different individuals,
120 between regions and across spatial scales of selection.

121 We used long-term monitoring GPS-data from adult lynx in two regions, one in southern and one in
122 northern Sweden, to investigate individual differences in resource selection and the efficacy of extrapolating
123 RSF estimates across different landscapes at varying scales of selection. We quantified resource selection at
124 two scales; home range distribution (second order) and within home-range (third order) selection (Johnson
125 1980). Our aims were to (1) estimate individual variation in habitat selection and its effect on the models'
126 predictive performance within the same geographic region, by quantifying variation in predicted RSF surfaces
127 estimated using different combinations of individuals; (2) quantify the ability to predict habitat suitability
128 using individuals from contrasting landscapes, by using the individual-based models from one study region to
129 predict suitable habitat in an alternative region; and (3) assess whether order of selection influences our ability
130 to accurately predict within and between regions.

131

132 **Methods**

133 *Study regions*

134 Two study regions were used for this study, one in southern and one in northern Sweden (Fig. 1a). Both
135 regions vary greatly from one another in terms of variables deemed relevant to lynx habitat selection (Table
136 1).

137 The landscape in the northern study region (Fig. 1b) is mountainous, with valleys at around 300 meters
138 above sea level (m a.s.l.) and high mountains reaching up to 2000 m a.s.l. (Rauset et al. 2013). At lower
139 elevations, bogs and lakes traverse the landscape, which is dominated by mixed coniferous forest consisting of
140 Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). At higher elevations, valleys and hillsides
141 birch forests (*Betula pubescens*) grow up to 600 – 700 m.a.s.l., followed by a low alpine tundra with thickets
142 of willow shrubs (*Salix spp.*) and dwarf birch (*Betula nana*) (Rauset et al. 2013). At higher elevations, lower
143 heaths and meadows grow while the mountain peaks and higher plateaus are characterized by bare rock and
144 glacier (Rauset et al. 2013). Infrastructure and human activity are very low in the northern study region
145 compared to southern Sweden, including a few settlements and roads, and virtually no agriculture. The main

146 prey for lynx in this area are migrating semi-domestic reindeer (*Rangifer tarandus*) managed by the
147 indigenous Sámi people (Mattisson et al. 2011).

148 Most of the southern study region (Fig. 1c) is relatively flat, with elevation levels increasing from the
149 southern to the most northern part of the southern study region, ranging from 0 to around 370 m.a.s.l. The
150 landscape is interspersed with lakes and largely covered with intensively managed forest (Norway spruce and
151 Scots pine interspersed with birch (*Betula sp.*)) (Andrén et al. 2002). In addition, fields traverse the landscape,
152 with agriculture and grassland covering 19% of the land (Hemmingmoore et al. 2020). Human population
153 density is high and increasing towards the south, and consequently there is a much denser network of cities
154 and towns, roads and highways in the southern compared to the northern study region. The main prey for lynx
155 in this area are roe deer (*Capreolus capreolus*) (Andrén and Liberg 2015).

156

157 ***Lynx GPS-location data***

158 The southern dataset is based on GPS-locations from 36 resident adult lynx (21 males and 15 females)
159 collected between 2008 and 2015 (Fig. 1c). The northern dataset is based on GPS-locations from 17 resident
160 adult lynx (eight males and nine females) collected between 2001 and 2010 (Fig. 1b). Where more than one
161 location per day was available for an individual, we randomly selected one location per day to reduce both
162 temporal autocorrelation and bias, which occurs when one individual is sampled more frequently than others
163 (Nielsen et al. 2002; Frair et al. 2004), resulting in 8,194 and 10,701 locations in the northern and southern
164 study region, respectively. All lynx were captured, immobilized, and fitted with GPS-transmitters (GPS plus
165 mini, Vectronics Aerospace, Germany; Televilt Posrec 300 and Tellus 1C, Followit, Sweden) according to
166 Swedish Animal Welfare Agency's ethical-approved protocols (Andrén et al. 2006; Arnemo and Fahlman
167 2009; Rauset et al. 2013).

168

169 ***Individual-based resource selection***

170 We *a priori* selected four environmental predictors shown to influence lynx habitat selection in a variety of
171 landscapes; 1) distance to forest edge (Niedziałkowska et al. 2006; Rauset et al. 2013; Samelius et al. 2013;
172 Zimmermann and Breitenmoser 2007), 2) distance to human infrastructure (which includes settlement, roads,

173 railways, and industrial sites) (Bunnefeld et al. 2006; Bouyer et al. 2015a; Gehr et al. 2017), 3) elevation
174 (Bouyer et al. 2015b) and 4) terrain ruggedness (Rauset et al. 2013; Bouyer et al. 2015b) (Table 1). Distance
175 variables were log-transformed ($\log(x+1)$), and all variables were scaled across both study regions prior to
176 analysis, to maintain comparability of results (Tables A4 and A5). For all variables, a resolution of 25 x 25
177 meters was used.

178 We used logistic regression in R (R Core Team 2018) to model RSFs for each of the two study regions
179 using a series of individual-based RSFs. The RSFs were based on a use-availability design, in which presence
180 points of the animal (hereafter “used points”) are compared to potential locations of an individual within the
181 landscape (hereafter “availability points”) (Boyce and McDonald 1999; Johnson et al. 2006; Manly et al.
182 2007). For each order of selection separately, available points were generated at random for each used point at
183 a ratio of 5:1 (Hemmingmoore et al. 2020). The same presence data was used for both orders of selection. To
184 quantify how animals select home-range placement within a larger landscape (second order selection) we
185 defined the second order available area by creating 95% minimum convex polygons around all individual
186 locations within each study region, scaling them up to 200%, merging them, and clipping the resulting
187 polygon by the Swedish border. Available locations were randomly generated from within this area (Fig 1;
188 dark grey). To assess habitat selection within the established home-range (third order selection), available
189 locations were randomly sampled for each individual from within their specific home-range, calculated as
190 95% minimum convex polygons around an individual’s locations (Fig 1; very dark grey). To quantify the
191 region-level distributions in beta coefficient estimates, we first ran individual-level RSF models. Secondly, we
192 bootstrapped coefficients by subsampling beta coefficients from the individual-level RSF models x times,
193 where x is 2 * number of individuals, and calculated the median value within the subgroup. This was repeated
194 10,000 times to obtain mean, standard deviation, median and confidence intervals for the beta coefficients
195 (Ladle et al. 2019).

196

197 ***Within region prediction of habitat suitability***

198 To assess to what extent regional RSFs are influenced by individual variation, for each study region and on
199 both orders of selection we randomly partitioned the individual lynx RSF predictions into two subsamples,

200 each consisting of 50% of the individual lynx. For each subset, we calculated a mean RSF value for each 25 x
201 25 m map pixel using the environmental predictors in Table 1, to create a spatial predictive surface for each
202 subset. We then obtained the Pearson correlation coefficient between the two surfaces. This process was
203 repeated 10,000 times for both the second and third orders of selection in both regions to obtain a distribution
204 of correlation coefficients based on multiple subsamples. To test the differences in the distribution of the
205 correlation coefficients between the second and third orders of selection for each study area, we subtracted the
206 third order distribution from the second order distribution to attain the probability density of their difference.

207

208 *Between region prediction of habitat suitability*

209 To test the ability of RSFs at predicting suitable habitat when extrapolating to a different location within the
210 species range, we 1) generated spatial predictive surfaces for both the northern and southern study region
211 based on the mean estimated RSF coefficients derived from all individuals within each study region, using the
212 available area in each study region (Fig. 1, the area within dashed lines), 2) calculated spatial predictive
213 surfaces for each study region using lynx from the alternate region and 3) estimated the overlap between the
214 areas of the highest 20% predicted values based on the model from each region itself and the model based on
215 the alternate region. This was repeated at both orders of selection.

216

217 **Results**

218 *Individual-based resource selection*

219 At the second order of selection, lynx in the north selected for ruggedness and against elevation and distance
220 to forest, whereas distance to human presence overlapped zero and was therefore neither selected for nor
221 against (Fig. 2a, Table A2). Lynx in the south also selected for ruggedness and against distance to forest.
222 Unlike in the north, southern lynx selected for increased distance from human infrastructure (Fig 2a). A high
223 variation among southern individuals regarding elevation resulted in no selection for or against at the regional
224 level (Fig. 2a, Tables A2).

225 At the third order of selection, the direction of selection in the north was retained for elevation,
226 ruggedness and distance to forest (Fig. 2b, Table A3). Northern lynx were again indifferent in terms of
227 selection of distance to human infrastructure (Fig. 2b). Southern lynx selected for ruggedness and distance to
228 human infrastructure. Coefficient estimates for both elevation and distance to forest overlapped zero
229 suggesting no preference, and there was high individual variation in their selection for elevation at the third
230 order, as at the second order (Fig. 2a).

231

232 ***Within-region prediction of habitat***

233 The ability of models to predict suitable habitat within the same region was slightly lower at the second order
234 compared to the third order of selection in both study regions (Fig. 3). Within the northern study area, 66% of
235 the 10,000 bootstrapped correlation coefficients for the third order of selection have a higher value than those
236 for the second order of selection. Within the southern study area, 91% of the correlation coefficients for the
237 third order selection are higher than those for the second order of selection.

238

239 ***Between region prediction of habitat***

240 In the northern study region, when comparing the area including the highest 20% RSF values of predictions
241 based on either northern or southern models, we found an overlap of 59.5% and 29.5% at the second and third
242 orders of selection, respectively (Fig. 4c, 4i). The expected overlap at random was 20 %. Models for northern
243 individuals predicted lower elevation valleys as high RSF values, while southern lynx models predicted the
244 western higher elevation, rugged regions to have high RSF values for lynx. This pattern was consistent,
245 irrespective of the scale of selection used (Fig. 4a, 4b, 4g, 4h, Figs. A1, A2).

246 In the southern study region, the highest 20% RSF values based on northern or southern models
247 overlapped by 49.9% and 59.5% at the second and third orders of selection, respectively (Fig. 4f, 4l). The
248 expected overlap at random was 20 %. Northern models failed to identify high RSF value patches in the center
249 of the southern study region, and estimated larger areas with very low elevation levels in the eastern part of
250 the southern study region as higher RSF values than southern models at both orders of selection (Fig. 4d, 4e,
251 4j, 4k, Figs. A1, A2).

252

253 **Discussion**

254 We used a long-term dataset of GPS-collared lynx collected from two study regions in Sweden with distinctly
255 different environmental characteristics, within the Scandinavian lynx population, to assess individual variation
256 in habitat selection as well as the ability to reliably predict suitable habitat when extrapolating RSF estimates
257 across contrasting landscapes at the second order (home range selection within the landscape) and third order
258 (within home range) of selection. Our findings showed that extrapolating data to other regions with different
259 ranges of environmental predictor values led to poor predictions of habitat suitability at both orders of
260 selection.

261

262 ***Within-region prediction of habitat selection***

263 We found low individual variation at both the second and third order of selection within both study regions for
264 the majority of coefficients (Fig. 2). The standard deviation increased at the second compared to the third
265 order for distance to forest and distance to human infrastructure, while for elevation and ruggedness in the
266 north, they remained similar between the two orders of selection (Table A2, A3). This indicates a higher
267 individual variation at the second order, which has indeed been observed in both study regions for all
268 variables, however to different extents (Fig. 2). From the third to the second order, individual variation in the
269 south increased most for distance to human infrastructure followed by elevation, in the north the highest
270 increase in individual variation was observed for distance to forest. However, the bootstrapped correlation
271 coefficients at the third order of selection were higher than at the second order of selection in both study areas,
272 indicating a potentially higher variation in habitat selected by individual lynx at the second order (Fig. 3).
273 Therefore, the scale of selection can influence the quality of predictive RSF models. High individual variation
274 within a few explanatory variables, e.g. distance to human infrastructure and elevation for southern
275 individuals at the second order (Fig. 2), were potentially enough to drive slightly lower correlation in the
276 predicted RSF values at the second order compared to the third order of selection. These results emphasize the
277 importance of visualizing and quantifying individual variation in habitat selection, rather than relying solely
278 on the mean values to represent the regional-level estimates and associated predictive surfaces.

279 A number of factors influence an individual's selection, including intraspecific competition, reproductive
280 status, sex, and hierarchical social structures within the population (Svanbäck and Bolnick 2007; Araújo et al.
281 2011; Tinker et al. 2012; Ladle et al. 2019). The effect of individual variation is however often ignored in RSF
282 modelling efforts, even when predicting within the study regions where individuals were sampled
283 (McLoughlin et al. 2010 but see Leclerc et al. 2016). Our results highlight that individual variation could in
284 fact influence the predictive performance of RSF models and that it should be considered when predicting
285 suitable habitat. One way of assessing individual variation and understanding its effect on predictions is the
286 approach taken here: estimating models at the individual level, constructing population-level coefficient
287 estimates and quantifying variance within estimates using a bootstrapping approach. This approach offers
288 potential to both predict regional-level RSF maps and individual variation around regional-level RSF maps.

289

290 ***Between region prediction of habitat***

291 Models performed poorly when used to predict RSF values in the contrasting study region (i.e. south
292 predicting north and north predicting south). Extrapolation from one area to another can lead to invalid
293 inference because the range of available resource values may not fully overlap between regions, thus forcing
294 the model to extrapolate its predictions to available values beyond those used to train it (Figs. A1 and A2).
295 Considering the second order of selection in our case study, lynx showed a positive selection for distance to
296 human infrastructure in the south, but the population mean used for predictions was negative in the north.
297 There is a high density of human infrastructure in the south and a very low density in the north (Table 1). As a
298 consequence, when southern models were used to generate predictions for the northern study region, they
299 overestimated RSF values, and northern models overestimate RSF values due to predicting selection against
300 greater distance to human infrastructure in the southern region. This example illustrates that one should avoid
301 including a variable with extremely low or non-existent values in one part of the studied region when
302 modelling suitable habitat, since it will confront the model with unknown values, thereby reducing the
303 model's predictive performance and reliability. Regarding elevation, the southern study region is relatively
304 flat, with value ranges falling largely below the northern values. Since northern lynx selected on average
305 against elevation, avoiding the very high mountain peaks in the northern study region, northern models

306 overestimated RSF values when extrapolated to the southern region. In contrast to northern lynx, the
307 population mean for southern individuals was positive for elevation at the third order of selection. This
308 suggests a quadratic relationship, meaning that lynx likely select for intermediate values of elevation at the
309 third order of selection. Because non-linear relationships have the potential to strongly impact the outcome of
310 habitat suitability predictions when extrapolating to regions which differ strongly in availability, this
311 comparison emphasizes the importance of understanding the effect of the availability distributions when
312 extrapolating. But even when individuals in both study regions select a resource in the same direction, the
313 availability distribution can affect the results. We found that northern and southern individuals both selected
314 for ruggedness at both orders of selection. However, because ruggedness availability values in the north vastly
315 exceeded those in the south, this further contributed to an overestimation of RSF values by southern models
316 when extrapolated in the north, despite the agreement in direction of selection.

317

318 *Effect of order of selection on predictions*

319 RSF estimates should start with a clear understanding of the species' ecology and the landscape from which
320 available values are being sampled; however the scale at which the analysis is taking place also informs the
321 results (Boyce et al. 2003; Boyce 2006; Fuller and Harrison 2010; DeCesare et al. 2012; Leclerc et al. 2016;
322 Holbrook et al. 2017; Reed et al. 2017). In our study, the predictive performance of the models were
323 potentially less accurate at the second order compared to the third order of selection within the same study
324 regions as judged by the probability densities of the correlation coefficients (Fig. 3, Table A2, A3). Larger
325 available areas at the second order could cover more diverse landscapes and hence a broader range of
326 available values relative to those found at the third order of selection. Therefore, higher landscape
327 heterogeneity at the second order has the potential to impact the reliability of habitat predictions on different
328 scales because individuals can select their habitat from a larger variety of resources at the second order
329 compared to the third order of selection. (Boyce et al. 2003, Herfindal et al. 2009; Bjørneraas et al. 2012).

330 When extrapolating predictions between the two study regions, we found an inverse effect based on study
331 region, with northern models being better in predicting habitat in the southern study region at the third order
332 of selection while southern models were more reliable in predicting habitat in the northern study region at the

333 second order of selection. Therefore, when extrapolating, the direction and also strength of selection has
334 potentially a higher impact on the predictions' outcome than the order of selection when extrapolating. This
335 further underlines the need to pay attention to a variable's available range and its implications for resource
336 selection between study regions with distinct environmental characteristics.

337

338 ***Conclusions and recommendations***

339 We used an extreme example of predictive RSF models presented in this case study to illustrate and discuss
340 potential drawbacks related to the extrapolation of RSF models and to highlight the need for caution,
341 especially when extrapolating RSF results to regions with different availability distributions from the source
342 region. This could be particularly useful to those considering the development of management strategies using
343 habitat predictions, e.g. to assess suitable habitat for species reintroduction, for the designation of protected
344 areas, or to predict range expansions or shifts.

345 First, it is important to be aware of any lack of overlap between available values used to fit the models
346 and the regions for which extrapolation is done, as values that fall outside of the range the models were
347 informed with will decrease the reliability of predictions. Consequently, there is a need to sample across a
348 gradient of available values for all the variables that will be used in the model, capturing as much landscape
349 heterogeneity as possible. When such a sampling scheme is not possible, for instance when predicting range
350 shifts based on climate scenarios (e.g. Li et al 2016) or predicting the establishment of an expanding
351 population (e.g. Inman et al 2013), it is important to discuss the limitations inherent in extrapolating beyond
352 the range of available values. Additionally, differences in management practices between regions can have a
353 large effect on habitat availability, e.g. if a species is excluded from areas that would otherwise provide
354 suitable habitat (e.g. Recio et al. 2018). This should be taken into consideration when projecting, for example,
355 areas for possible re-establishment since the exclusion of a species from regions within the study region can
356 bias a species' used locations relative to the assumed available landscape (Eriksson and Dalerum 2018),
357 adding further error to estimated habitat suitability. In our example, all models tended to misidentify habitat
358 suitability when extrapolating to other areas. Hence, there would have been the risk that an area would be
359 designated for protection although it does not provide adequate habitat for the species of conservation

360 concern, or that individuals would be released in areas that had been misidentified as suitable. Therefore,
361 extrapolations should ideally be limited to areas where the range of available values for the variables used are
362 overlapping those of the study region upon which the original RSF is based, to increase transferability and
363 reliability of the models' predictions.

364 Second, because resource selection is scale-dependent, it is important to apply a multiscale approach
365 within resource selection studies to ensure that patterns of habitat use are accurately described and that the
366 appropriate scale to answer the research or management question at hand is chosen (Boyce 2006, Manly et al.
367 2007, DeCesare et al. 2012; Northrup et al. 2013). Moreover, to allow an adequate reflection of resource
368 selection across a heterogeneous landscape, an effort should be made to minimize any spatial bias in sampling
369 individuals, to obtain a distribution as uniform across the relevant landscape as possible, which we
370 acknowledge can be difficult.

371 Third, while literature regarding habitat predictions often include maps indicating the area of data origin
372 as well as the area of extrapolation, it is not common practice to report the values ranges of variables used to
373 fit the model as well as the range of variables in the extrapolation area (Schadt et al. 2002; Kuemmerle et al.
374 2011; Falcucci et al. 2013; Inman et al. 2013; Bleyhl et al. 2015; Eriksson and Dalerum 2018). The inclusion
375 of such information (Tables A1, A4 and A5) would however be useful to understand the reliability of the
376 predictions.

377 Increasing the transparency of research regarding the data and methods used to generate habitat
378 predictions will contribute to the credibleness of the analysis conducted. By doing so, users are more likely to
379 identify the order of selection which is more relevant to the research or management question as well as to
380 avoid the false identification of unsuitable habitat as suitable when extrapolating data.

381

382 **Declarations**

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388 ***Conflicts of interest***

389 The authors have no conflicts of interest to declare that are relevant to the content of this article.

390 ***Ethics approval***

391 All lynx were captured, immobilized, and fitted with transmitters according to Swedish Animal Welfare
392 Agency's ethical-approved protocols (Arnemo and Evans 2017).

393 ***Consent to participate***

394 Not applicable

395 ***Consent for publication***

396 Not applicable

397 ***Availability of data and material***

398 The datasets generated during and/or analyzed during the current study are available in the figshare repository
399 at DOI 10.6084/m9.figshare.14823690.

400 ***Code availability***

401 The code used during the current study is available in the figshare repository at DOI
402 10.6084/m9.figshare.14823690.

403 ***Authors' contributions***

404 This study was conducted within long-term research projects led by HA and JP. The original concept for this
405 study was proposed by HH, and all authors contributed to the design. Material preparation and data collection
406 were performed by MA, JP and HA. The analysis was performed by AL, AP, HH, and MA, with support from
407 HA. The first draft of the manuscript was written by AP with support from HH, MA and AL. All authors
408 contributed to subsequent versions of the manuscript, and all authors read and approved the final version of
409 the manuscript.

410

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Figures

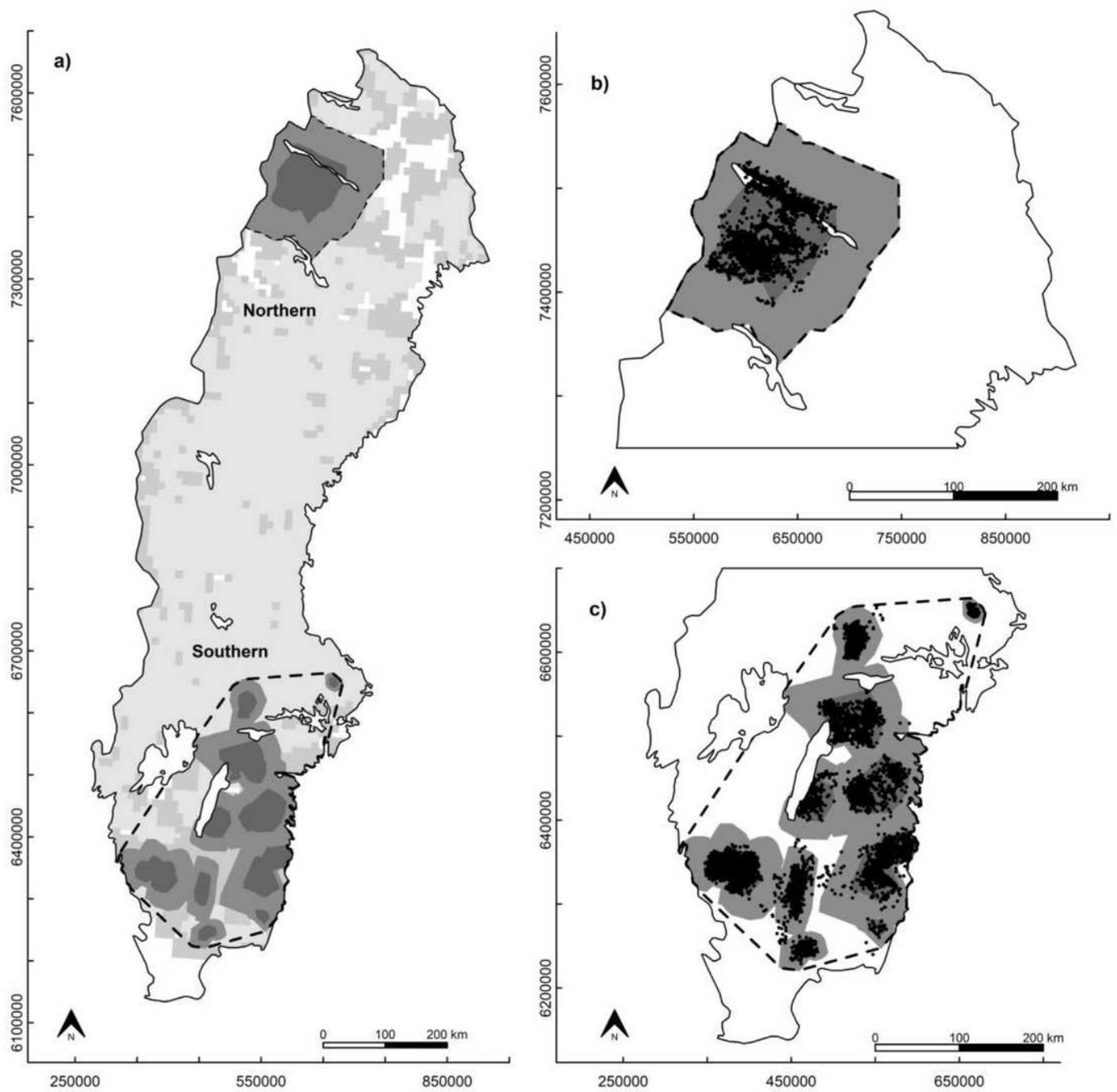


Figure 1

a) Sweden with permanent lynx distribution (very light gray), sporadic lynx distribution (light gray), overlapping 95% MCP lynx home ranges (very dark gray) representing the available area for 3rd order selection in the northern and southern study areas respectively, and with available areas for 2nd order selection (dark gray). Maps b) and c) show the northern and southern study areas, respectively, with

used points (black), available area for 3rd order selection (very dark grey), and available area for 2nd order selection (dark grey). Dashed lines indicate the available area used to predict suitable habitat

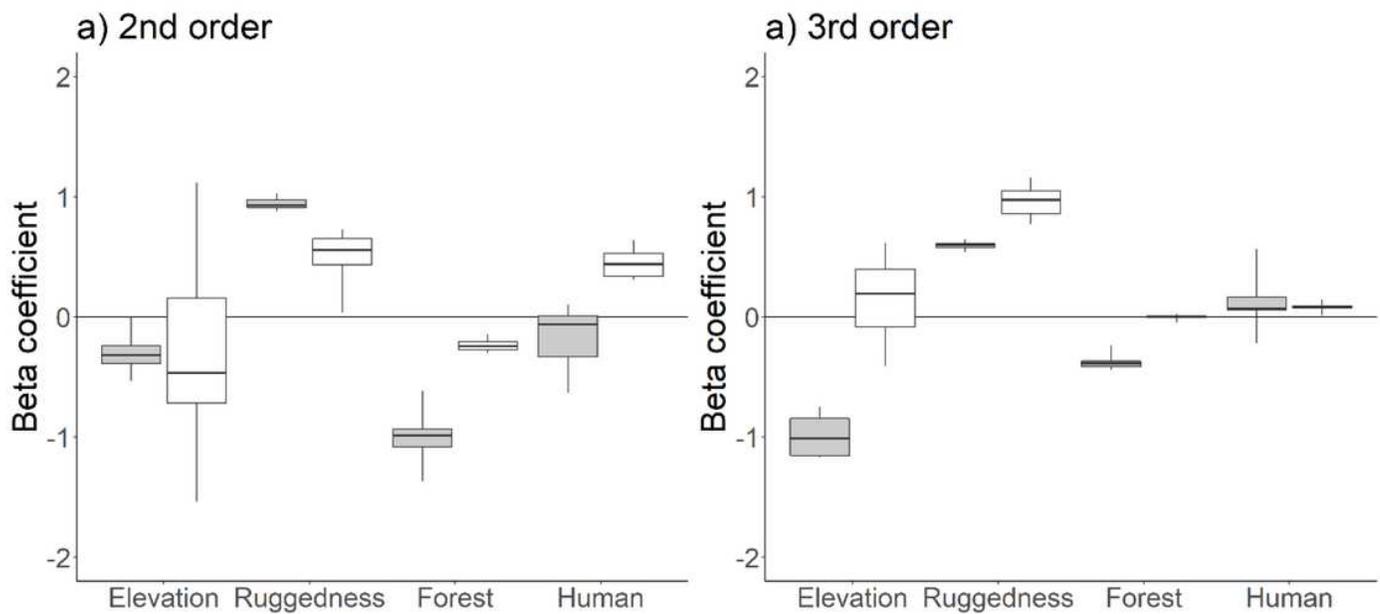


Figure 2

Boxplots of the bootstrapped beta coefficients of the environmental predictors elevation, ruggedness, distance to forest (Forest) and distance to human infrastructure (Human) for 2nd order of selection and 3rd order of selection. Grey (left boxes) represents the northern lynx and white (right boxes) the southern lynx

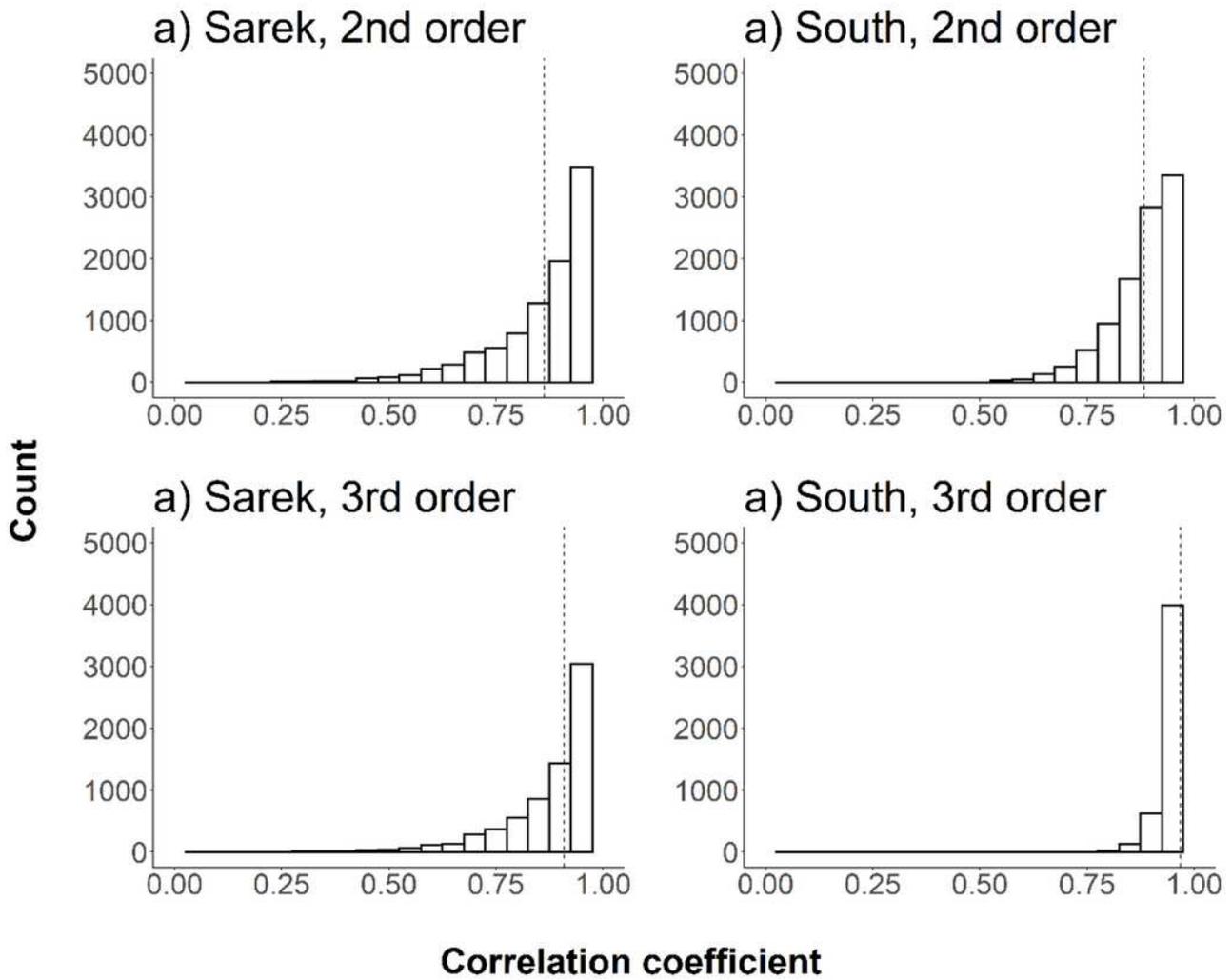


Figure 3

Correlation coefficients between sets of individual lynx for 2nd order selection and 3rd order selection. Dashed lines represent the mean correlation coefficient. Grey represents northern lynx and black represents southern lynx

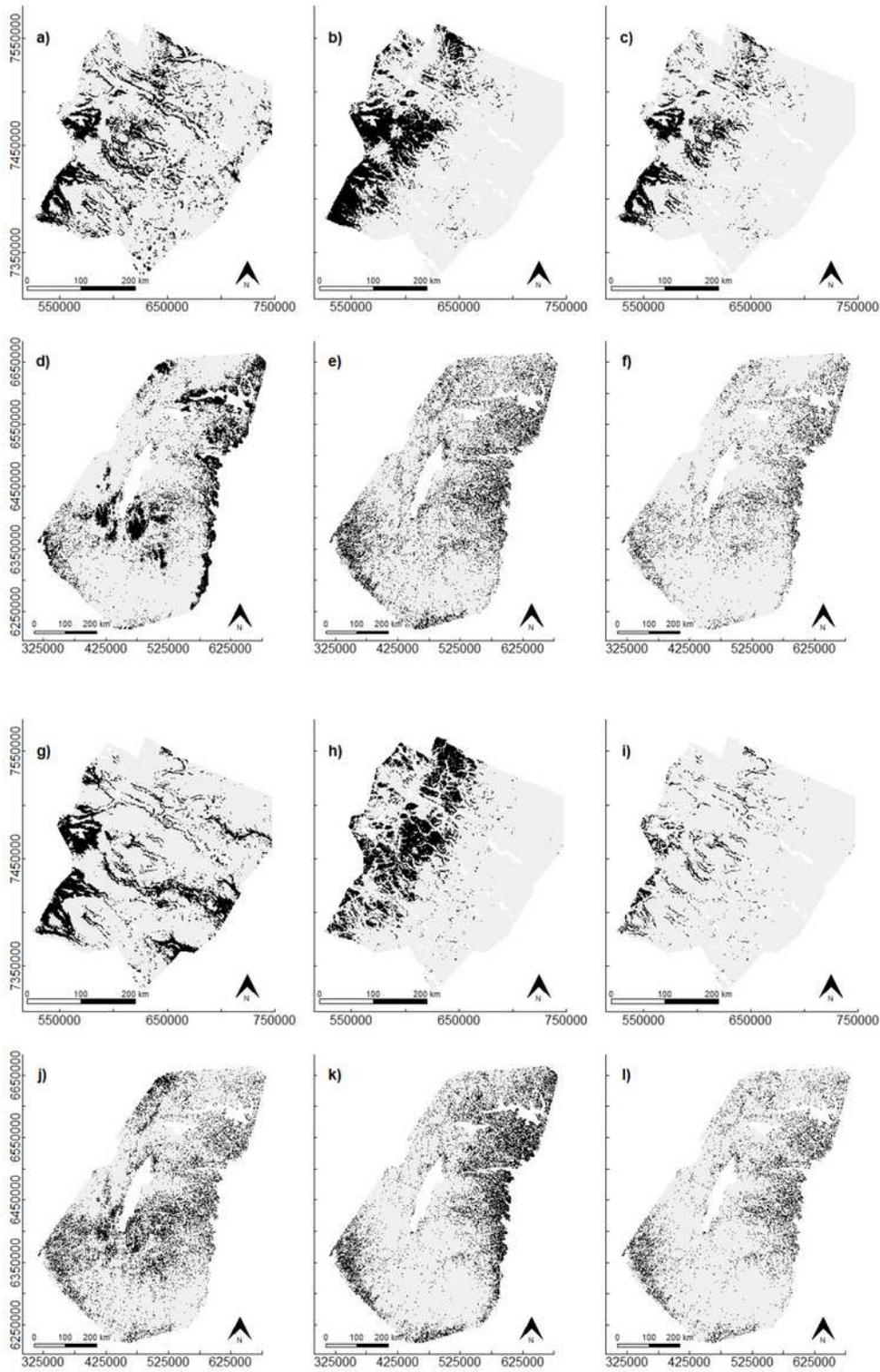


Figure 4

Maps indicating the top 20% of RSF-values for both study regions on both orders of selection (black; left and middle column) as well as the overlap between patches of high RSF-values by both original and external models (dark grey; right column). Maps a – f represent 2nd order selection; a) north based on northern models, b) north based on southern models, c) overlap of high RSF-values in the north based on either northern or southern models, d) south based on southern models, e) south based on northern

models, f) overlap of high RSF-values in the south based on either northern or southern models. Maps g – l represent 3rd order selection; g) north based on northern models, h) north based on southern models, i) overlap of high RSF-values in the north based on either northern or southern models. j) south based on southern models, k) south based on northern models, l) overlap of high RSF-values in the south based on either northern or southern models

Supplementary Files

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