



Searching for the fundamental niche using individual-based habitat selection modelling across populations

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Strictly speaking, fundamental niches are inestimable. Nevertheless, ecologists attempt approximating them to understand species' distribution and plasticity to environmental changes, with invaluable repercussions on both theoretical and applied ecology. So far, individual-based habitat selection models only characterized realized niches of populations delimited by physical (e.g. fences), historical (colonization) and biotic (competition) barriers constraining access to a subset of resources available to the species. As populations with different realized niches share the same fundamental niche, we developed a novel framework to scale-up response curves from population-scale habitat selection models to approximate the species' optimal habitat choices, unbiased by barriers constraining accessibility. We used GPS-locations from 147 wild mountain reindeer *Rangifer t. tarandus*, belonging to 7 of the remaining populations scattered throughout the subspecies' range. We linked individual choices to accessible habitat features using conditional-logistic regression with log-link function in a use-available design. Focal variables were modeled using 2nd degree polynomials on log-scale, which correspond to a Gaussian curve used to approximate the fundamental niche optimum (curve mean) and breadth (variance). Using both real and simulated data we demonstrate that robust approximations of a fundamental niche optimum and breadth can be estimated using a relatively small number of representative populations with relatively few individuals. While each classical realized niche model had strong predictive power for the focal population but poorly predicted across populations, the approximation of the fundamental niche allowed for robust inter-population comparisons in habitat quality. The proposed approach brings individual-based habitat selection models forward along the continuum from investigating the realized niche of a population towards investigating a species' fundamental niche, and allows us to quantify empirically the relationship between realized and fundamental niches. This allows improving the understanding of differences in fitness among populations, the prediction of species' distributions and plasticity to environmental changes, and suggestions for mitigation priorities.

The fundamental niche has been defined as the 'n-dimensional hypervolume [...] every point in which corresponds to a state of the environment which would permit [a species] to exist indefinitely' (Hutchinson 1957). In other words, the fundamental niche is a theoretical construct defined in environmental space (as opposed to 'geographic space', both defined in Peterson and Soberón 2012), describing the set of conditions ('...any property outside the organism under consideration') allowing a species to have a positive growth rate. Hence, identifying a species' fundamental niche would allow understanding its requirements and predicting its distribution in geographic space under altered past, present or future environmen-

tal conditions (Buckley 2008), with major theoretical and applied consequences for a range of disciplines such as conservation ecology, community ecology, global change biology and landscape management. However, strictly speaking a complete Hutchinsonian hypervolume is intrinsically inestimable for two reasons (Whittaker et al. 1973). First, its estimation would need to rely on observations of realized niches, in which the species is bound by an intricate web of biotic and abiotic constraints (Soberón 2010). Hence, measurements of the species' response to each variable would be biased by their intrinsic correlational structure (Whittaker et al. 1973). Second, the number of axes composing the hypervolume in environmental space is virtually infinite. As a consequence, fundamental niches cannot be properly predicted in geographic space, as it is not possible to identify all areas characterised by all combinations of biotic and abiotic conditions where the species could persist (Soberón 2007, Peterson et al. 2012).

Unaffected by these limitations, the hunt for the fundamental niche is intensifying, and researchers attempt to make

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the challenge more achievable by focussing on an increasing (Blonder et al. 2014) but still low number of key variables using a multitude of approaches (Soberón and Peterson 2005). Mechanistic approaches focus on the underlying processes driving patterns and hence, all other things being equal, they should be the most rigorous and robust when extrapolating beyond the observed conditions. These models aim at scaling up the responses of individual traits like survival or reproduction to the full range of environmental variation, measured under controlled conditions (Kearney and Porter 2004). Although in recent years mechanistic niche modelling has been advancing within theoretical frameworks of biophysical ecology, nutrition, and dynamic energy budget, due to the complexity of the task these models are applied only to simple organisms and to a narrow set of traits and variables (Kearney et al. 2010, Barve et al. 2011, Jankowski et al. 2013). Besides, ethical and practical issues would render the required experimental manipulations unfeasible for most animal species, especially those of conservation issue. Finally, as mechanistic approaches are based on physiological variables, they inherently ignore biotic interactions and ‘have little hope of taking them into account’ (Soberón and Peterson 2005). Hence, notwithstanding their stronger theoretical justification and the fact that they promise higher predictive power in altered ecological conditions compared to phenomenological (or statistical) models, no comparative assessment has been produced so far, and Schoener’s (1986) ‘mechanistic ecologist’s utopia’ is yet to be attained (Kearney et al. 2010).

Commonly, two types of correlative approaches are used to investigate ecological niches. The first is a group of static, probabilistic techniques for species’ distribution modelling, relating the observed geographical distribution of (frequently sessile) organisms to their present environment (Guisan and Zimmermann 2000, Thuiller et al. 2009). The second group of techniques applies to vagile species and uses individual-based movement data, commonly collected remotely, to measure the extent to which animals are selective in their habitat use (Manly et al. 2002). Hence, this second approach uses spatio-temporal information on individual behavioural responses to the available range of values for a given set of biotic and abiotic conditions, and thus holds a much greater potential to understand the mechanisms generating space use patterns. Both approaches rely on the assumptions that individuals have the possibility to respond (either through their vital rates and/or movements) to the full range of available values for a given variable, and that their locations or environmental choices reflect their ecological requirements. The latter assumption is most often true; in our case for example Nilsen et al. (pers. comm.) found a good correspondence between habitat quality (estimated by the model presented here) and fitness-related parameters. However, the former assumption is regularly violated due to historical (e.g. colonization history), biotic (e.g. competition, predation), or physical (e.g. fences, oceans) barriers to dispersal, which prevent assessing individual response curves to the full range of accessible values for a given variable. Consequently, both correlational approaches only describe the reduced hypervolume in which a species or population exists – i.e. the realized niche – but failed so far to reveal the species’ fundamental niche (Guisan and Zimmermann 2000, Peterson and Soberón 2012). The problem is less marked when modelling

species’ distribution in a macro-ecological framework for sessile species with limited dispersal abilities, as the wide-ranging datasets commonly used minimize the differences between realized and fundamental niches. Hence, the ‘fundamental niche’ concept appears often in the jargon of species’ distribution modelling. On the contrary, the issue becomes more severe when using individual-based movement data which, until recently, have been available only for limited spatio-temporal windows (Hirzel and Le Lay 2008). Hence, individual-based studies typically refer to a small subset of the conditions potentially available to the species and, thus, virtually always avoid the fundamental niche concept. In the last decade however, the widespread use of animal-borne technologies such as GPS devices has made available massive amounts of high-resolution individual-based movement data, which no longer represent a major limiting factor for the study of animal–habitat relationships (Hebblewhite and Haydon 2010). What is still lacking is a theoretical framework for scaling-up movements of individuals to infer the species’ habitat preferences and, ultimately, fitness (Gaillard et al. 2010, Morales et al. 2010, Owen-Smith et al. 2010). Although variations in habitat selection related to availability are well documented (Fortin et al. 2008, Mayor et al. 2009), to our knowledge no solution has been proposed so far to overcome the limitations imposed by physical (e.g. fences), historic (e.g. colonization) or biotic (e.g. competition) constraints to movements and move individual-based habitat preference studies along the continuum leading from investigating the realized niche of a population towards approximating the species’ fundamental niche.

As Hutchinson (1957) observed, the fundamental niche is the volume in the environmental space that permits positive probability of survival of a species. Such volume is delimited by the ‘zero net growth isocline’ (Tilman 1980), where the species’ growth rate is null ($dN/dt = 0$; Fig. 1). Within this line, or ‘envelope’ (Hirzel and Le Lay 2008), heterogeneous environments provide a gradient in environmental conditions ranging from an optimum, allowing the species to reach its highest growth rate, to suboptimal conditions, allowing the species to persist without growing. A niche is thus delimited by the zero net growth isocline, and its’ shape is defined by its optimum and breadth. Identifying the envelope is challenging, as it would require knowledge of population growth rates with respect to each combination of environmental conditions – which is hard to obtain for wild animals. On the contrary, information on the niche optimum and breadth can be obtained through the analysis of animal behaviour. Ideally, to achieve this one should quantify the response curves of individuals exposed to the full range of available environmental conditions with respect to each variable. However, few (if any) individuals or populations can choose among the full range of variability for a given variable, while for most the choice is constrained by accessibility. When the accessible area does not include the niche optimum, individuals are expected to display a monotonic response to the focal variable. If optimal habitat is accessible, animals are expected to show non-linear responses with a peak in proximity of the niche optimum (Fig. 1). Following Whittaker et al. (1973), we argue that whenever experimentation is not possible the fundamental niche may be approximated only through a generalization of all measurable realized

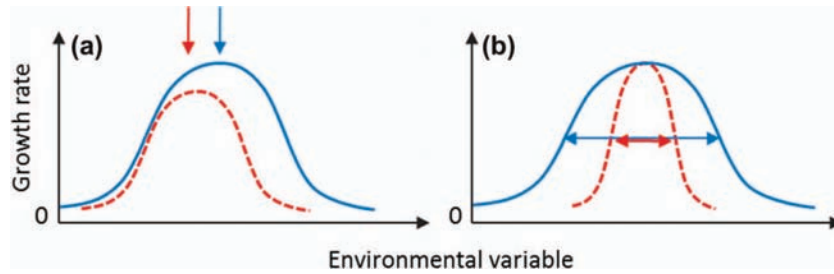


Figure 1. For each environmental variable, a niche can be represented by a Gaussian curve delimited by its envelope (i.e. the value that the function asymptotically approaches far from the peak – 0 in the figure), and shaped by the curve's optimum (or mean, indicated by the arrows, in (a) and breadth (or variance, (b)). Within the range of values of the fundamental niche of a species (blue), the realized niche of a population (red) can have a different optimum, and narrower breadth.

niches of the species' populations. Hence, we developed an approach to combine the response curves of individuals/populations exposed to different means and ranges of availability for each variable into one response curve that approximates the species' optimal values and tolerance thresholds, i.e. the fundamental niche optimum and breadth.

As a case study we used GPS-locations from 147 wild mountain reindeer *Rangifer t. tarandus*, belonging to 7 of the last remaining populations, to approximate the subspecies' niche optimum and breadth within the distribution range, in south Norway. Archaeological data and recent studies show that before industrial development Norwegian wild reindeer were grouped into intermixed population units performing massive seasonal migrations between adjacent mountain systems (Vistnes et al. 2004, Panzacchi et al. 2013b). Largely due to the development of infrastructures, mainly along valley bottoms, Norwegian wild reindeer can no longer follow most of their traditional migration routes and are now divided into more than 20 virtually isolated sub-populations confined within areas which do not necessarily provide optimal amounts of both summer and winter pastures. Using data from the largest and most representative sub-populations, we aimed at characterizing and predicting both all sub-populations' present realized niches and approximating the species' fundamental niche, i.e. the environmental preferences reindeer would exhibit if there were no barriers to movements – which would correspond to reindeer movement behaviour before industrial development. We predict that each realized niche model will have a good predictive power for each focal population for which it was developed, but will poorly predict across populations. On the contrary, we predict that the approximation of the fundamental niche model will produce more robust predictions at the species' level, thus allowing for inter-population comparisons in habitat quality.

The realized niches were identified straight-forwardly by comparing used to accessible habitat within each of the sub-populations, which are primarily delimited by transportation infrastructures (Panzacchi et al. 2013b; no inter-specific competition occurs in the mountain). To identify the species' fundamental niche we extrapolated behavioural choices of individuals 'trapped' in different sub-populations and, therefore, exposed to a limited amount of the environmental variation occurring throughout the species' range. To strengthen and generalize the applicability of our approach we explored the amount of data needed to obtain reliable estimates for niche parameters. Recent studies demonstrated

that the ability to detect habitat selection is influenced by both the number of individuals tracked and tracking frequency, with the former being substantially more important above a certain threshold in tracking frequency (Börger et al. 2006, Girard et al. 2006). We go further and investigated through both simulations and real data the effect of adding more individuals and more populations, with differing ranges of habitat availability, on the estimation of niche parameters.

Methods

Study area

Norwegian wild reindeer are divided into more than 20 isolated populations, each occupying a dedicated management area in southern Norway; we studied 7 of the largest populations during winter (Fig. 2a, b). Although management areas span a wide range of environmental characteristics, they are mostly located above the tree line and are influenced by an east-west climatic gradient, with the western part subjected to oceanic influences characterized by abundant rain and snow precipitation and the eastern part experiencing more continental climate. Also an east-west gradient in terrain ruggedness can be identified, with more rugged terrain and higher mountain peaks in the western areas close to the fjords, compared to the less rugged terrains in the mountain plateau in the east (Bakkestuen et al. 2008).

Each management area is largely delimited by transportation infrastructures, which strongly constrain wild reindeer movements (Panzacchi et al. 2013b). Reindeer are the only ungulate inhabiting the harsh Norwegian mountain plateau; hence, no inter-specific competition occurs. Predation is an irrelevant cause of mortality for wild reindeer; however, golden eagles *Aquila chrysaetos* occasionally prey upon calves, and wolverines *Gulo gulo*, which are mainly scavengers, have been reported killing reindeer. The main reindeer mortality factor is hunting, which keeps densities well below carrying capacity – thus preventing strong density-dependent feedback effects.

Reindeer GPS data

GPS data were collected for 147 adult females belonging to 7 of the largest and most representative management areas

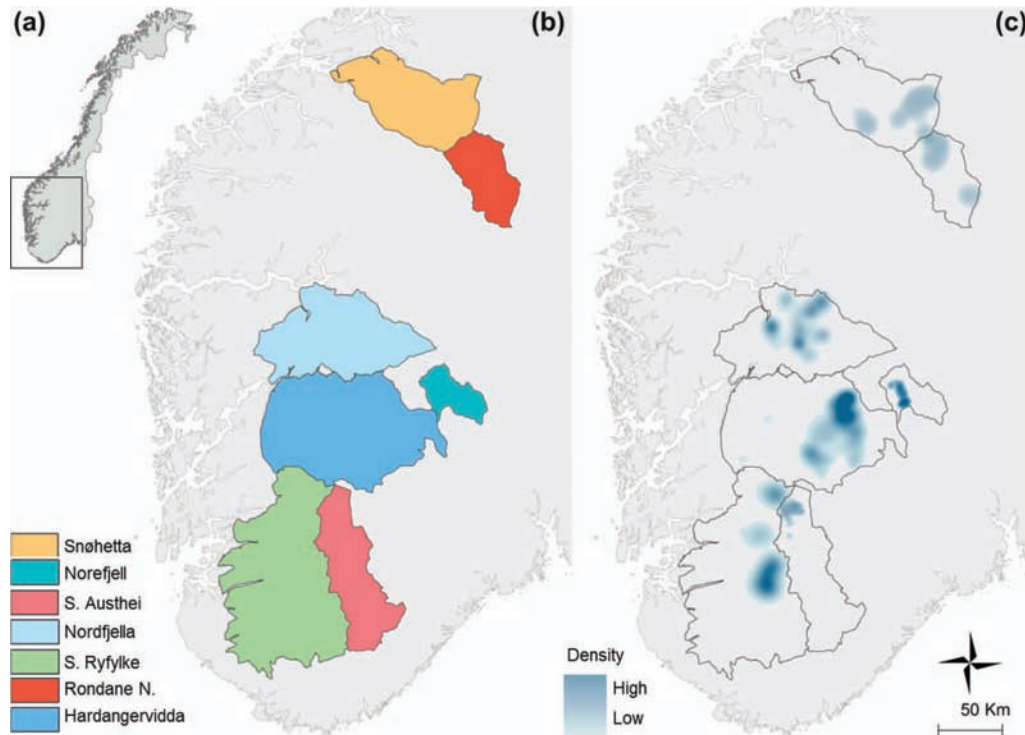


Figure 2. Distribution range of wild mountain reindeer in Norway – which coincides with their European distribution range (a) – and detail of the study areas, which consists of 7 of the largest and most representative wild reindeer management areas (b). In (c) are illustrated, for each management area, the home ranges of wild reindeer females during winter estimated using kernel UD 95%.

(Fig. 2): S. Ryfylke (15 deer, study period 2006–2010), S. Austhei (9, 2007–2010), Hardangervidda (48, 2001–2010), Norefjell (10, 2005–2007), Nordfjella (19, 2007–2010), Snøhetta (19, 2009–2010) and Rondane N. (27, 2005–2010). Reindeer were immobilized from helicopter (details: Evans et al. 2013) and equipped with GPS collars with drop-off systems. Due to the large amount of data, for each individual we selected only 1 GPS location every 6 h. In this paper we focused on winter, which is the limiting season for reindeer, but parallel studies are estimating year-round niches. January was taken as representative of the winter season, to avoid including data from the end of autumn migration or from the beginning of the spring migration. We used the R code provided in Bjørneraas et al. (2010) to identify and remove a few outliers (i.e. errors in GPS locations); the code calculates trajectory-based metrics to identify locations arising from highly unrealistic movement patterns. Data processing and analyses were performed using R.3.0.1 (2013).

Environmental layers

We linked individual habitat choices to accessible habitat represented by trophic resources, climate, topography, and man-made infrastructures. Bakkestuen et al. (2008) synthesized the variation in the major environmental gradients in Norway into four principal components, PCs, accounting for 75 to 85% of the variation. The four resulting maps (PC1, 2, 3, 4; 1 km resolution), reflect the major environmental gradients in the study area. PC1 indicates a regional gradient from coast to inland and from oceanic/humid to

continental areas (oceanic-continental gradient); PC2 indicates regional variation from north to south and from high to low altitudes (alpine-nemoral gradient); PC3 represents topographic (terrain relief) variation on finer scales than the other PCs (high-low terrain ruggedness); PC4 represents regional variation from north to south and from inland to coast in solar radiation (high-low solar radiation gradient). We used PC1 and PC2 because the oceanic-continental gradient and the altitudinal gradients have been long referred to as driving factor for seasonal migrations in reindeer. PC3 and PC4 were chosen, respectively, because the access to sub-nivean vegetation is facilitated in wind-blown ridges, and in sunny areas favoring snow-melt. We also used a vegetation map, NORUT (Johansen 2009, resolution 30×30 m), identifying 25 vegetation types including lichen mats, heather, etc. As proxies of human disturbance we used the density of public and private roads, skiing and hiking trails, private cabins, tourist cabins and power lines. The densities of point and line features were calculated with ESRI ArcMap 10.0 within different search radii (1, 2, 3, 5, 10, 15 km); we let the model identify the most relevant scale for each variable (see next paragraphs). Variables were standardized to mean 0 and standard deviation 1.

Defining accessibility

Selection occurs when a given habitat is used disproportionately compared with its availability, the latter being the amount accessible to the animal (Beyer et al. 2010). Hence, defining accessibility is a crucial step in selection studies.

Underestimating availability would lead to underestimate selection, while overestimating it including suitable not-accessible habitat would yield misleading results (Barve et al. 2011). If, for example, reindeer were confined to areas without lichens (preferred winter fodder) and we would include non-accessible areas containing lichens, the model would erroneously conclude lichen avoidance. Notwithstanding the importance of correctly defining accessibility, no tools are available to do so. Hence, accessibility was defined for each population based on results of previous studies (Panzacchi et al. 2013a, b) showing avoidance of transportation infrastructures, steep ridges and glaciers in our study area, and low or null probability of crossing of roads and railways (see also Reimers and Colman 2006, Vistnes and Nellemann 2008). We first identified areas actually used by radio-monitored individuals from each given population, and we delimited along the closest road, fjord or glacier. Note, however, that such delimiting features were included in the accessible area, to allow the model detecting responses to them. Hence, we obtained 7 (at times slightly overlapping) accessible areas, one for each of the studied populations (Fig. 2a).

Modeling the species' fundamental niche and the populations' realized niches

We attempted to model the fundamental niche of wild reindeer in Norway using conditional logistic regression (CLR) with a log-link function in a use-available design, using the *coxph* function from the 'survival' library (Therneau and Lumley 2009). CLR is similar to ordinary logistic regression, except that observations are grouped into strata and a separate baseline probability (i.e. intercept) is fitted to each stratum. Each individual location was paired with 10 available points randomly sampled within the population range to which that individual belonged; each group (1 used + 10 available points) represented a stratum. Hence, CLR compared only (i.e. conditioned) the characteristics of points used by each individual with those available within the population range to which that individual belonged to. Note that no individual or population identifiers directly entered the model. To account for differences in the number of observations between populations we weighted each observation so that each population contributed equally to the model. Hence, the model estimates one single response curve for a 'typical' Norwegian reindeer, based on the combination of the responses of each animal at each given time to what was available in that given population.

While for most variables we expected linear responses (and we included them using linear terms), for PCs 1–4 we expected non-linear response curves, and we thus modelled niche optimum and breadth. Following Austin (1999), a niche can be approximated with a Gaussian curve with the optimum represented by the curve mean μ and the breadth represented by the variance σ^2 (Fig. 1). As a Gaussian curve on a linear scale equals a second degree polynomial on a log scale, we modeled Gaussian shaped response curves using second degree polynomials:

$$y = \beta_1 \times X + \beta_2 \times X^2 \quad (1)$$

on a log-scale, and we included in the model both the linear and the quadratic terms. We then calculated the niche optimum μ , and breadth σ_s^2 , with respect to each variable of interest using the regression coefficients:

$$\mu_s = \beta_1 \times \sigma^2 \text{ (or, } \mu_s = -\beta_1 / (2 \times \beta_2)) \quad (2) - \text{ niche optimum}$$

$$\sigma_s^2 = -1 / (2 \times \beta_2) \quad (3) - \text{ niche breadth}$$

Note that the niche breadth will only be defined when $\beta_2 < 0$, as only then the curve has a Gaussian shape; the larger the coefficient in absolute value, the larger the niche. Note also that quadratic terms should be avoided whenever the estimated optimum falls outside the range of available values. To avoid this problem, we first set up a model using quadratic terms and we performed a preliminary model selection. After, we calculated μ , and made sure that it fell within the range of available values; if not, the quadratic term was not included in the full model. To ensure comparability of the results, we adopted a similar modeling approach and used CLR also to estimate each population's realized niche; in this case, however, calculations were done separately for each population.

Selection of variables and model selection

As some of the proxies of human disturbance were correlated, we calculated the residuals of the regressions between correlated variables: 1) density of tourist cabins and trails (rTrails); 2) density of private roads, public roads and private cabins (rPrivRoad); 3) density of power lines and public roads (rPowerLine). We selected the most influential radius of influence for each variable through a preliminary model selection, and we used it to initialize the full model, as follows. First, we calculated residuals at matching radii for the density layers (e.g. rTrails, with both cabins and trails calculated within 1 km), we built univariate models using each radius, and we selected the model with lowest Akaike information criteria, AIC. If the sign of a coefficient changed from negative to positive for increasing radii, we selected the model with lowest AIC among those with negative coefficients, as a change in sign would reflect changes in the ecological meaning of that variable (Polfus et al. 2011). Then, we used the selected radii to recalculate the residuals (e.g. rTrails, with cabins at 1 km and trails at 5 km). Disturbance variables calculated in this way entered the full model together with PCs and vegetation classes from the land cover map (excluding one class representing the intercept). We started a backward iterative model selection procedure by removing variables with a Variance Inflation Factor (VIF, which measures how much the variance of an estimated regression coefficient is increased because of collinearity; Kutner et al. 2004) above 5, and we further reduced this model. We repeated the selection of the best disturbance radius for the reduced model, and we reiterated the previous steps until the model no longer changed. Finally, to account for temporal autocorrelation in the residuals we calculated robust standard errors following Forester et al. (2009), and we removed from the model variables non-statistically different from zero.

Model validations

We performed model validations for both the realized and the fundamental niche models by classifying predicted preference values into 10 equal-sized categories, and by calculating the Spearman correlation coefficient between these categories and the proportion of used versus available points in each category – averaged over populations for the fundamental niche model. In addition, similar to Boyce et al. (2002), we further validated the fundamental niche model using cross validation: we parameterized the model by excluding one of the populations in turn, predicted in the population excluded and compared these predictions with the classified data as described above. We also cross-validated the realized niches parameterized on one population, and predicted values from each of the other populations were compared to the classified data as described above.

Effect of adding populations/individuals to the estimation of niche parameters

We used both simulations and real data to understand the effect of adding individuals (or locations) and populations on the estimation of the linear and quadratic terms (Eq. 1) and, consequently, on the estimation of the fundamental niche optimum and breadth (Eq. 2 and 3). Different simulated individuals ($n = 500$, each contributing with 100 locations) and populations ($n = 50$, each containing 10 individuals) were assigned different means and ranges of availability for a hypothetical environmental variable. For each individual/population we generated used points, sampled using the species' Gaussian curve as a probability function, and available points, obtained by randomly sampling within the range of availability for each individual. Used and available points were paired and used as a dependent variable in a CLR, as described above. When using simulated data the regression was reiterated 10 000 times by randomly taking an increasing n of individuals (from 10 to 500) or populations (1 to 50). Note that the results of the individual/population simulations are comparable, as the total number of locations is the same (50 populations corresponds to 500 individuals). As the number of individuals varies among populations, when using real data we calculated regressions for all possible combinations of individuals at increasing steps, from 1 to the total number of individuals for that population.

Results

The winter realized niche models for each of the 7 populations differed largely with respect to which variables were included and their effect sizes, and also differed from the winter fundamental niche model (Supplementary material Appendix 1, Table A1, Table A2), supporting that realized niches are constrained by geographical barriers. The realized niche models showed that most populations show optimal preferences with respect to the oceanic-continental continuum, which is clearly shifted towards continental areas (Fig. 3a, Supplementary material Appendix 1, Table A2); accordingly, the fundamental niche model shows an optimum close to continental end of this continuum (Fig. 3a).

On the contrary, although no population showed an optimal altitudinal preference within the available area (Fig. 3b, Supplementary material Appendix 1, Table A2), the fundamental niche model was able to identify an optimal altitude, clearly shifted towards higher-altitude areas, as expected in this season (Fig. 3b, Supplementary material Appendix 1, Table A2). Note that Fig. 3 shows the range of values available to each population (e.g. Norefjell has a small range of available areas all shifted towards the continentality end of the continuum, Fig. 3a), but does not inform about mean values or shape of the distribution; thus, it is interesting to pinpoint that the only population showing preference for lower-altitude areas inhabits the highest mountain range (Fig. 3b, Snøhetta). The prediction from the fundamental niche model suggests that in absence of barriers large amounts of preferred winter habitat would be located on a large mountain plateau (Hardangervidda) in the south, and on the continental side of the northern area (Rondane N; Fig. 4a). On the contrary, in Ryfylke (south-west) there is a high discrepancy between realized and fundamental niche, suggesting that this population would have migrated to areas with better winter habitat if not constrained by physical or behavioral barriers (Fig. 4a, b).

Both fundamental and realized niche models performed well, as both models succeeded in capturing the most used areas within each population. Validation revealed that models performed well. The correlation coefficient between the average proportion of pixels used in each study area and the predicted habitat preference according to the fundamental niche model was high (Spearman rank test $\delta = 0.985$, $p < 0.001$; coefficients ranged from $\delta = 0.83$ to $\delta = 0.98$). The results of the cross validation also supported the robustness of the fundamental niche model ($\delta = 0.964$, $p < 0.001$; coefficients ranged from $\delta = 0.64$ to $\delta = 0.97$). The Nordfjella population had the lowest fit ($\delta = 0.64$), likely due to changes during the study period that affected availability differently for different individuals.

The correlations between the proportion of pixels used within each management area and the predicted habitat preference according to the realized niche models were also high: Rondane N: $\delta = 0.969$, $p < 0.001$; Snøhetta: $\delta = 0.969$, $p < 0.001$; Nordfjella: $\delta = 0.969$, $p < 0.001$; Norefjell: $\delta = 0.937$, $p < 0.001$; Hardangervidda: $\delta = 0.988$, $p < 0.001$; S. Austhei: $\delta = 0.610$, $p = 0.061$; S. Ryfylke: $\delta = 0.996$, $p < 0.001$). As expected, when using each of the 7 realized niche models to predict in each of the other 6 areas we recorded wide variability in the validation coefficients, which ranged from $\delta = -0.418$ to $\delta = 1.000$ (average: 0.79 ± 0.26 SD).

The effect of sample size in simulated and real data

Analyses of simulated data demonstrated that both estimates for the niche optimum and breadth started stabilizing after adding a relatively small number of populations (Fig. 5b) and individuals per population (Fig. 5a). The precise number of populations and individuals required to obtain stable estimates depends on the level of precision required by each research project, and Fig. 5 should serve as a basis for inferring the sampling regime required to obtain the desired level

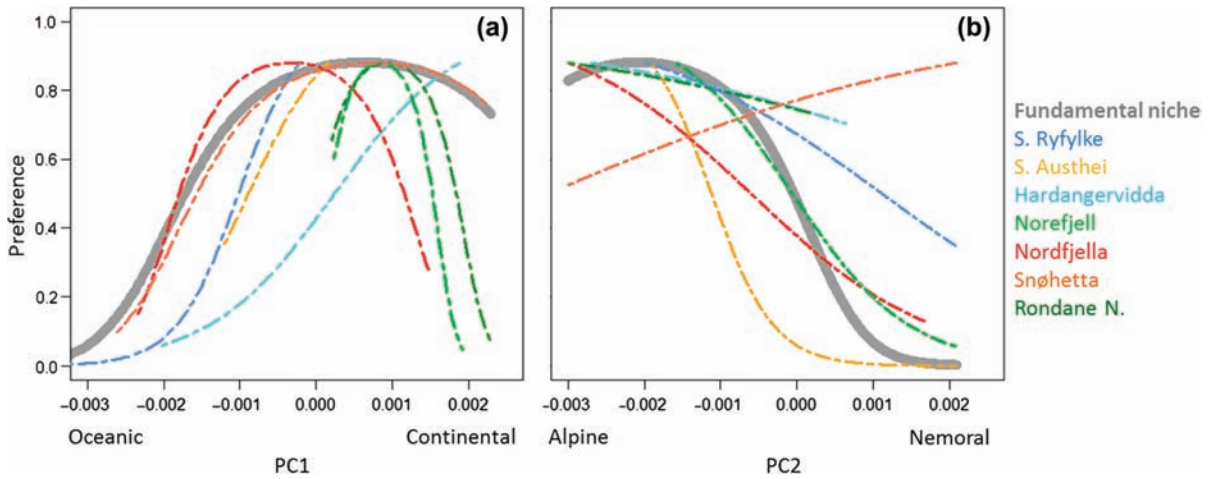


Figure 3. Response curves to PC1 (oceanic-continental gradient, (a)) and to PC2 (alpine-nemoral gradient, (b)), as predicted by the approximation of the fundamental niche model (thick line, grey) and by the 7 realized-niche models for each of the studied populations (colored) during winter.

of precision. Using real reindeer data, the estimation of the fundamental niche optimum and breadth for two of the environmental variable used in the models, PC1 and PC2, started to stabilize after adding ca 4 populations (Fig. 6; see Fig. 1 for effect of sample size of individuals). Thus, although we used a fairly low number of populations ($n = 7$), the fundamental niche model appeared to be robust. The observed effect of adding more individuals on the parameter estimates

for each population is shown in Supplementary material Appendix 1, Fig. A1.

Discussion

Although strictly speaking a comprehensive characterization of an Hutchinsonian fundamental niches is unfeasible, the niche concept can be rephrased operationally to describe a

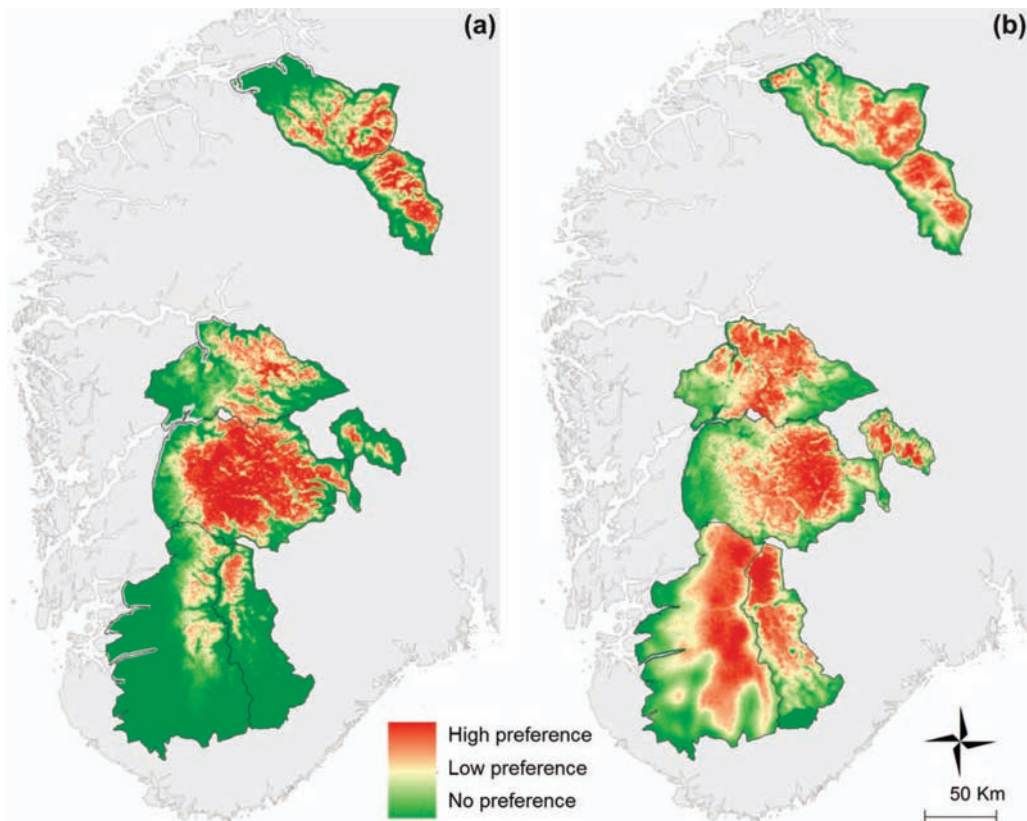


Figure 4. Model prediction for the approximation of the fundamental niche of wild mountain reindeer in Norway during winter (a), and model predictions for the 7 realized niches of each of the studied reindeer populations during winter (b).

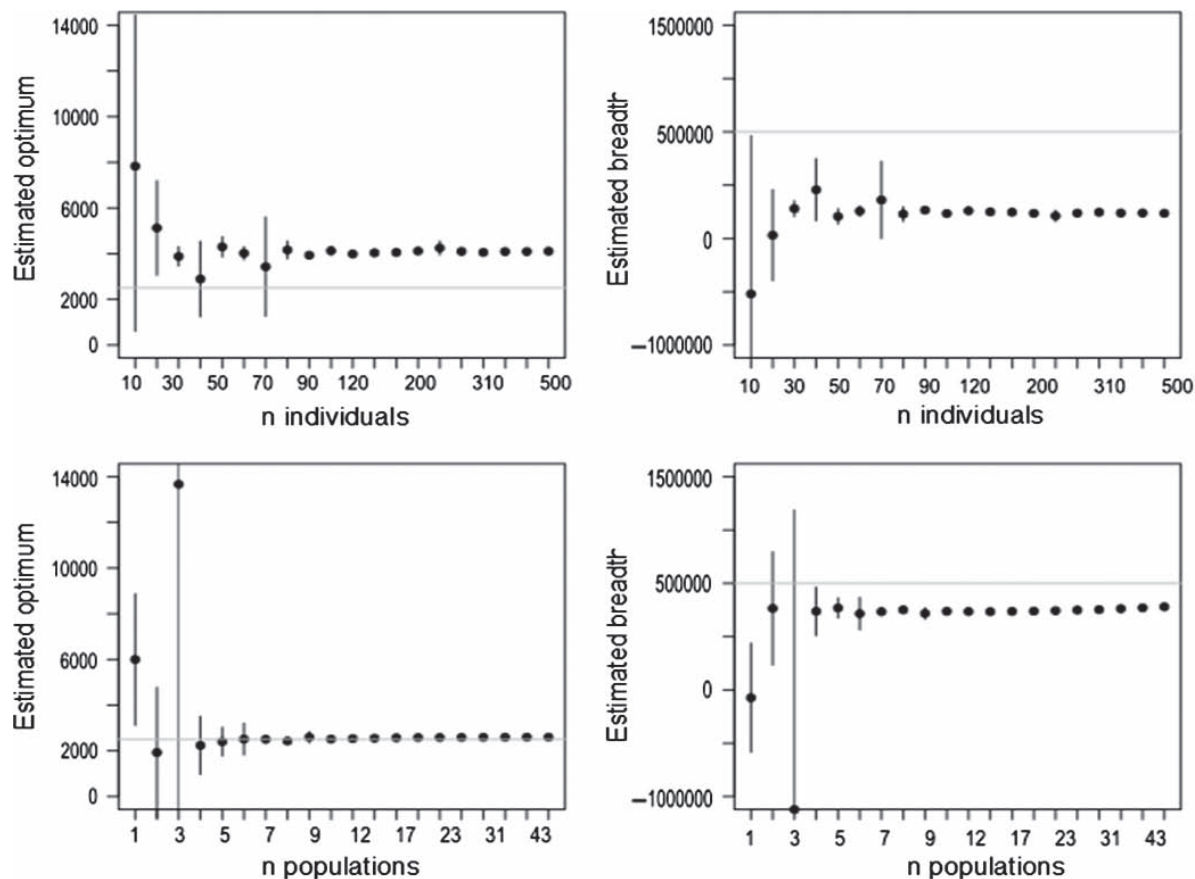


Figure 5. Simulations illustrating the effect of increasing the n of individuals (from 10 to 500, each contributing with 100 locations; top panels), or of populations (from 1 to 50, each population contributing with 10 individuals each with 100 locations; bottom panels) on the estimation of the fundamental niche optimum (Eq. 2, left) and breadth (Eq. 3, right). This figure can support the identification of the appropriate sampling regimes for obtaining estimates of niche optima and breadth with the level of precision required by different research projects. For each parameter set we performed 10 000 simulations. For each simulation set we display the mean and twice the associated standard error; the horizontal line shows the true values in the simulations. Note that simulating 10 individuals with 100 locations each corresponds to simulating 5 populations with 200 locations each.

subset of environmental space corresponding to geographic areas where a population (in the case of realized niche) or species (fundamental niche) can persist indefinitely (Soberón 2007). Within this operational framework, we developed a novel approach to extrapolate from a patchwork of realized niches of populations distributed throughout the species' range to obtain the closest representation of a species' fundamental niche to date for large animals (Fig. 4a). Furthermore, we show empirically the relationship between fundamental and realized niches – the latter being subsets of the fundamental niche (Fig. 3). This has several crucial theoretical and applied implications. For example, as predicted by Peterson et al. (2012), it may lead to the identification of some portions of a fundamental niche which may actually not exist anywhere on Earth, or that have not been yet observed within the sampled realized niches. On a practical perspective, the comparison between fundamental and realized niches can lead for example to the identification of populations inhabiting sub-optimal ranges, which would allow making research-based decisions on conservation priorities and developing targeted and cost-efficient mitigation measures.

Within each area, both realized and fundamental niche models performed well, by highlighting similar optimal and

sub-optimal areas used by reindeer. Note, however, that due to its larger and more representative sample size, the fundamental niche model is less likely to suffer from problems related to co-linearity of explanatory variables and to over-fitting, which may bias classical realized-niche models developed for smaller areas. As expected, the approximation of the fundamental niche model provided invaluable additional information compared to the realized niche models at the species' range scale. In our case study each of the 7 realized niche models (Fig. 4b) well described population distribution (Fig. 2c) within each area for which it was built, but failed in predicting across populations. On the contrary the approximation of the fundamental niche model (Fig. 4a), in addition to well characterizing population distribution within each area, allowed advancing our understanding of the species' potential distribution in absence of spatial constraints. In particular, the model produced robust, nation-wide predictions providing the unprecedented opportunity to contrast reindeer management areas in terms of habitat quality. This showed that while some populations inhabit optimal winter ranges (e.g. Hardangervidda), others are 'trapped' in sub-optimal winter areas (e.g. Ryfylke), with potential consequences on carrying capacity and fitness parameters of the

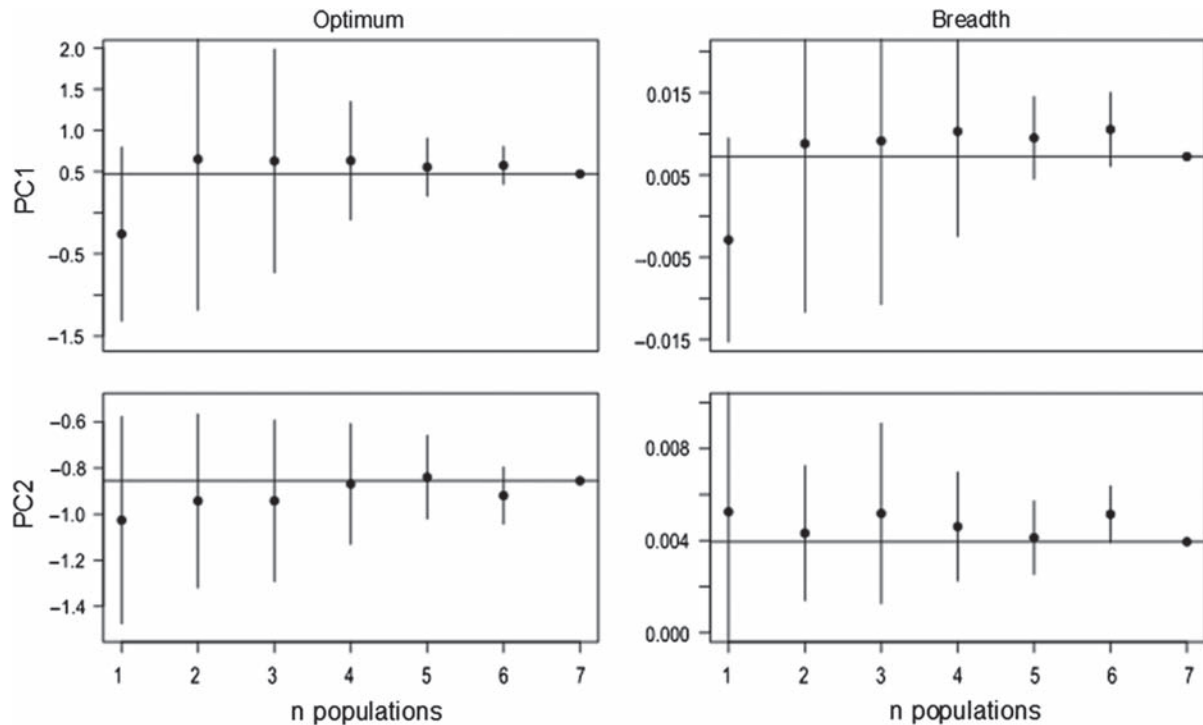


Figure 6. Observed effect of increasing the number of reindeer populations (from 1 to 7, the latter is the total n of populations in the study) on the estimation of the linear and quadratic terms (Eq. 1) and on the estimation of the fundamental niche optimum and breadth (Eq. 2 and 3, respectively), for two of the environmental variables used in the models: PC1 (oceanic-continental gradient) and PC2 (alpine-nemoral gradient; Bakkestuen et al. 2008). The mean estimate from all combinations of populations is shown with the standard deviation around this mean. The horizontal line represents our best estimate, obtained using all 7 populations.

population living therein. Indeed, parallel studies have demonstrated a link between the observed differences in fitness among populations and differences in range quality as indicated by the approximation of the fundamental niche model (Nilsen et al. pers. comm.). Furthermore, the comparison among areas in terms of seasonal habitat quality allowed us to understand the drivers of past seasonal migrations, now lost largely due to the construction of infrastructures. For example, the scarcity of optimal winter habitat in Ryfylke explains the reasons of past seasonal migrations of this population towards the neighbouring Hardangervidda plateau, as also demonstrated by archaeological findings (Panzacchi et al. 2013b). Hence, the approximation of the fundamental niche model provided invaluable information to identify populations and areas to be prioritized for management, conservation and mitigation actions.

Simulations of synthetic data (Fig. 5 bottom) and movement data from isolated populations scattered throughout the subspecies' range (Fig. 6), demonstrated that a good approximation of the fundamental niche can be robustly and rapidly estimated by including a relatively limited number of new populations, each composed by relatively few individuals. Note that although the parameters' precision increases also with the addition of individuals from a single population (Supplementary material Appendix 1, Fig. A1), their accuracy does not improve substantially after a certain threshold, and their real values may never be correctly estimated (Fig. 5, top). Hence, not only is the ability to correctly estimate habitat selection more influenced by the number of individuals than by tracking frequency (now that

GPS-technology allows for quite high tracking frequency; Börger et al. 2006, Girard et al. 2006), but we also demonstrated that it is more affected by the addition of individuals from different populations, rather than from more individuals from the same population. The number of individuals or populations needed to robustly identify niche optimum and breadth depends largely on the level of precision required by different research projects. The results of the simulations in Fig. 5 aim at supporting project leaders in identifying the appropriate sampling regime (i.e. decide where to intensify the sampling effort in terms of individuals or in which area to start new telemetry studies) for obtaining estimates of niche optima and breadth with the required level of precision. In our case, both the simulations (Fig. 5, 6) and the analysis of real data (Supplementary material Appendix 1, Fig. A1) show that the 7 populations used in this study, with on average 21 individuals per population – each tracked over multiple years – seem sufficient to obtain stable and reliable parameter estimates.

Several challenges still need to be tackled to increase precision and accuracy in the search for the niche optimum and breadth. In particular, we envision the need to investigate the sensitivity of niche parameters to: 1) the addition of individuals/populations with different variability in resource availability; 2) behavioral variability among individuals/populations (e.g. some of our reindeer populations used to be semi-domestic, and thus seem to respond differently to disturbance; Reimers et al. 2012); 3) differences in density among population, with consequent repercussions on niche breadth (Van Horne 1983, McLoughlin et al. 2010);

4) different assumptions in terms of niche shapes (Hirzel and Le Lay 2008), including the possibility of holes (Blonder et al. 2014); 5) interactions between predictors. Finally, one should note that our approach allows approximating niche optimum and breadth, but it does not provide information regarding the niche 'envelope' or 'zero net growth isocline' (Tilman 1980, Hirzel and Le Lay 2008). Indeed, the Gaussian curves' breadth calculated in Eq. 3 equals the niche breadth for each possible envelope, and thus the actual niche breadth of a given species depends on both Eq. 3 and on the envelope. In other words, we identify the continuum between optimal and sub-optimal areas and we can thus compare niche optimum and breadth across populations (Fig. 4), but we cannot identify precisely the 'zero net growth isocline' (i.e. the cutoff line between source-sink areas). Ongoing studies integrating animal spatial behavior and population dynamics can help solving this challenging task (Nilsen et al. pers. comm.), which represents one of the main frontiers in ecology (Boyce et al. pers. comm.).

Still, we believe that the approximation of the fundamental niche, as provided here, is a major step in reliably predicting the potential distribution of a species and its tolerance to environmental changes. On a more general perspective, we believe that the search for the fundamental niche using individual-based models is worth pursuing, as it allows scaling up from classical habitat selection studies, concerned with habitat use given availability (often in fragmented landscapes), to fundamental niche studies, concerned with potential habitat use if animals could act in an unconstrained manner. This would open for the possibility to test for a wide range of hypotheses relating optimal habitat choices to fitness, investigating deviations from the ideal free distribution across populations (Galanthay and Flaxman 2012), and assessing species' plasticity to natural and man-made environmental changes.

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Supplementary material (Appendix ECOG-01075 at <www.ecography.org/readers/appendix>). Appendix 1.