Coexistence of large mammals and humans is possible in Europe's anthropogenic landscapes

Authors: Benjamin Cretois[1]; John D. C. Linnell[2]; Bram Van Moorter[2]; Petra Kaczensky[2]; Erlend B. Nilsen[2]; Jorge Parada[3]; Jan Ketil Rød[1]

Affiliations:

[1] Department of Geography, Norwegian University of Science and Technology, 7491 Trondheim, Norway

[2] Norwegian Institute for Nature Research, PO Box 5685, Torgard, 7485 Trondheim, Norway

[3] Department of Mathematical sciences, Norwegian University of Science and Technology, 7491 Trondheim, Norway

Corresponding author:

Benjamin Cretois

e-mail: benjamin.cretois@ntnu.no

keywords:

adaptation, sustainability, Europe, ungulates, carnivores, human disturbance, human-wildlife conflicts, human-wildlife coexistence

Abstract

Aim:

A critical question in the conservation of both large carnivores and wild ungulates is where they are able to live. In Europe, large mammals have persisted, and recently expanded, alongside humans for millennia, but surprisingly little quantitative data is available about large scale effects of human disturbance on their broad scale distribution. In this study, we quantify the relative importance of human land use and protected areas as opposed to biophysical constraints on large mammal distribution.

Location:

Europe.

Time period:

Recent.

Major taxa studied:

Large mammals.

Methods:

We analysed recently compiled data on large mammals distribution (both large ungulates and large carnivores) using random effects GLM along with dominance analysis to quantify the relative effect of anthropogenic variables on species' distribution. We finally quantify the effect of anthropogenic variables on the size of the species' niche by simulating a scenario where values of anthropogenic variables are set to zero.

Results:

We found that the broad scale distribution of most large mammals in Europe includes areas of high to very high human disturbance. Their distribution is primarily driven by environmental variables rather than the human footprint or the presence of protected areas. Furthermore, our counterfactual scenario provide evidence that anthropogenic variables hardly influence the area of species' distribution.

Main conclusions:

We suggest that coexistence between large mammals and humans is primarily determined by the willingness of humans to share multi-use landscapes with wildlife rather than the ability of wildlife to tolerate humans.

1. Introduction

Biodiversity is declining in most parts of the globe as a consequence of a growing human population and increasing per capita consumption with all its associated direct and indirect impacts on wildlife (Pimm et al., 2014). This trend is accelerating, and the most recent IPBES report estimates that 25 per cent of assessed animal and plant species are threatened by local or global extinction (Díaz et al., 2020). As species diversity supports a wide range of ecosystem services (e.g pollination, food, aesthetic appreciation) and especially large mammals have a range of consumptive and non-consumptive values for people (Linnell et al., 2020; Ripple et al., 2014) its loss would have dramatic impacts on our societies, and governments are urged to implement biodiversity conservation measures.

Even though most conservation actions have the primary objective of safeguarding the long-term persistence of wildlife, a lot of debate centers around the most effective strategies (e.g. land sharing vs land sparing). Some conservationists advocate a focus on implementing a spatial dichotomy, where “wild areas” would be subject to minimal human intervention (land sparing) and would act as a refuge against human disturbance for wildlife. Alternatively, another paradigm consists of a diversity of coexistence strategies (land sharing), which envisions the possibility of shared landscapes where human and wildlife interactions are allowed, managed and sustained by effective institutions (Carter & Linnell, 2016). Both approaches trigger a lot of debate among conservationists. Current legislation in most countries mandates wildlife conservation throughout the entire multi-use landscape with the possibility for sustainable use of wildlife, while it additionally sets aside a minimum proportion of the land as protected areas (Cretois et al., 2019).

Adopting a land sharing strategy requires a mutual adaptation in behavior from both humans and wildlife (Carter & Linnell, 2016). This may seem especially challenging for large animals as they are more likely to be negatively impacted directly (e.g. through persecution and exploitation) and indirectly (loss and fragmentation of habitat and introduction of invasive species) by human activities due to their larger spatial and resource requirements and the potential for human-wildlife conflicts (Redpath et al., 2013). In fact, because of their size, large animals with wide-ranging behavior and slow reproductive rates are frequently at risk of extinction (Ripple et al., 2014; Ripple et al., 2015).

Coexistence with large mammals has been a historical challenge in Europe. Large carnivores were extensively persecuted in retaliation for killing livestock while large ungulates were overexploited for sport hunting and meat. This resulted in populations of both taxa being driven to the edge of a near continent-wide extinction in the early 20th century (Chapron et al., 2014; Apollonio et al., 2010). Even though European landscapes are among the most affected by humans (Venter et al., 2016), strict regulations, reintroduction programs, effective wildlife management institutions, reforestation and agricultural abandonment have allowed large mammals to recover. Nowadays, these species are again found across very large areas of the European landscape (Chapron et al., 2014; Linnell & Zachos, 2010). Although there is an increasing body of literature addressing the impacts humans have on large mammals (Tucker et al., 2018; Carter et al., 2012; Alexander et al., 2016) , we are not aware of any attempts to quantify the extent to which the contemporary recovering distributions of large predators and their prey in Europe are directly limited by the presence of humans and their habitat modifications as opposed to underlying biophysical constraints. The issue is important in order to understand the factors limiting the potential for large scale coexistence in a crowded and human-modified continent.

In this study we evaluate the relative effects of both the human footprint and protected areas compared to the effects of environmental variables such as climate and terrain on large mammal distribution at a continental scale. We use hierarchical Bayesian models to estimate the importance of these variables on species' distributions and compare the environmental niche of these species with and without accounting for human variables by simulating a scenario where the European landscape is free of human influence.

2. Material and Methods

2.1. Distribution data

In this paper we focus on wild large mammals which are native to Europe and whose distribution is not intensively managed (i.e. excluding the European bison *Bison bonasus,* Linnell et al., 2020). This includes ten large ungulates in Europe: roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), moose (*Alces alces*), wild reindeer (*Rangifer tarandus*), Alpine chamois (*Rupicapra rupicapra*), Pyrenean chamois (*Rupicapra pyrenaica*), Alpine ibex (*Capra ibex*), Iberian ibex (*Capra pyrenaica*) and wild boar (*Sus scrofa*). We extracted the distribution data provided by Linnell et al. (2020) for all these species. Because the distribution of the mountain ungulates is restricted and because several species belong to the same genus and have similar ecological requirements, we merged the distribution of the Iberian and Alpine ibex, and the distribution of the Alpine and Pyrenean chamois creating *Capra* spp. and *Rupicapra* spp distributions. Distribution data for the four species of large carnivore present in Europe; wolves (*Canis lupus*), Euroasian lynx (*Lynx lynx*), brown bears (*Ursus arctos*) and wolverines (*Gulo gulo*) were derived from published data (Chapron et al., 2014). Distribution data for all species were the most up-to-date available and had a spatial resolution of 10km x 10km, although it must be born in mind that the underlying distribution data is of widely varying quality and resolution. The 10km x 10km resolution allow the results of our analysis to be comparable to other large scaled studies such as Tucker et al., 2018 or Chapron et al., 2014. We were able to include data on both herbivores and carnivores from 31 countries, consisting of all EU countries (excluding Cyprus and Malta), plus Norway, Switzerland, Serbia, Albania, Northern Macedonia and Kosovo.

2.2. Explanatory variables

We collected three abiotic covariates that are thought to be influential drivers of species distribution at biogeographic scales and two anthropogenic covariates.

Terrain Ruggedness Index and the Potential Evapotranspiration for the Warmest Quarter (PETWQ) were acquired from the ENVIREM dataset (Title & Bemmel, 2018) at a spatial resolution of 2.5 arc minutes (i.e. about 3km x 3km at 50°N). The mean snow cover duration (SCD) was derived from the Global SnowPack, a 14 year average available at a 0.25km x 0.25km resolution (from 2000 to 2014; Dietz et al., 2015). We used PETWQ and SCD as proxies for summer and winter severity respectively. Snow depth is widely viewed as being a major limiting factor for species latitudinal and altitude distributions as it correlates with cold winter temperatures, and the physically inhibition of animal movement and access to forage (Leblond et al., 2010). Evapotranspiration serves as a proxy for hot, dry, unproductive summer conditions that also limit species through thermal stress, water access, and poor forage conditions (Tattersall et al., 2012). Terrain ruggedness is widely viewed as being an important escape terrain for species (especially ibex and chamois) to avoid disturbance and predation (Nellemann et al., 2007). These three bioclimatic variables were all obtained as raster data.

As a measure of human disturbance, we chose the Human Footprint Index (HFI; Venter et al., 2016). Ranging from 0 to 50, the HFI is a raster representing multiple variables related to human disturbance (e.g. the extent of built environment, cropland, pasture land, human population density, nighttime lights, railways, roads and navigable waterways; Venter et al., 2016).

Finally, we obtained the protected area coverage from the World Database on Protected Areas: https://protectedplanet.net/). We selected all terrestrial designated protected areas in Europe (i.e. we excluded protected which category was either “Not Reported”, “Not Applicable” or not “Assigned”). Data was available as vector data and was rasterized at a resolution of $1km^2$ using ArcGIS Pro for ease of computation. The value 1 was assigned to grid cells located inside a protected area and 0 otherwise. Although European protected areas are almost never wilderness areas (Linnell et al., 2015) they are expected to be associated with greater restrictions on human activities that could potentially better limit human impacts on wildlife, and less intensive forms of land use.

We assessed the extent of collinearity between the covariates. Winter and summer severity were negatively related (r = -0.71), as both display strong coastal-inland and north-south gradients. However, we opted to include both as they reflect different mechanisms for species' ecology. Following Dormann et al., 2013 we made sure to carefully interpret the results of these two variables by interpreting the combined effects of all environmental variables. Other covariates were not significatively correlated with each other (r < 0.70; Table A1 in Annexes). We aggregated all the explanatory variables to the same 10km x 10km grid cell resolution.

2.3. Statistical analysis

2.3.1. Model specification

Because the residuals of the non-spatial models were strongly spatially correlated we fitted an intrinsic conditional autoregression (iCAR) model using hierarchical Bayesian models for each of the 13 species. The probability of presence (π) of a given species in a given grid cell was calculated using a Bernoulli distribution and the following model:

$$y_i \sim Bernouilli(\pi_i)$$

$$logit(\pi_i) = \alpha_i + x_i\beta + u_i$$

Where x_i is the vector of covariates for cell *i*, β the vector of parameters to be estimated and u_i the spatially correlated random effect whose prior is defined as:

$$u_i|u_k \sim normal(\frac{\sum_{i \neq k} w_{i,k}\, u_k}{n_i}, \frac{\sigma_u^2}{n_i})$$

Where $w_{i,k} = 1$ if grid cells *i* and *k* are neighbors and 0 otherwise. n_i is the total number of neighbors of grid cell *i*. We define two cells as being neighbors if they directly share a single boundary point. All models assume a vague prior for the regression parameters $\beta \sim normal(0,\ 1000)$ and we used a penalized complexity prior on the spatial effect to avoid risks of overfitting (See supplementary material).

As we expect species to have an optimal niche for environmental variables we included linear and quadratic terms for winter and summer severity and ruggedness (Svenning et al., 2011). We also included linear and quadratic terms for human footprint as we suspected certain species to have an optimal niche in the moderate human disturbance level. We only included a linear effect for protected area coverage as we only expected a linear response.

To fit the spatial models, we used the Integrated Nested Laplace Approximation (INLA) approach with the package R-INLA (Lindgren & Rue, 2015). INLA is a faster alternative to Markov Chain Monte Carlo approaches and yields similar, if not identical, results (Beguin et al., 2012). We standardized the covariates to enable direct comparison between the regression coefficients. All analyses were conducted in R 3.6.1.

We validated the models by plotting residual values against covariates for each model. We also plotted the leave-one out cross validation scores (conditional predictive ordinate CPO in this case) to estimate model fit.

2.3.2. Evaluation of variables' importance for species' distribution

We estimated the relative importance of both environmental and anthropogenic variables using dominance analysis (Azen & Budescu, 2003), which is a procedure to quantify variable importance through examination of the R^2 values (or similar metrics) for all possible subset models of a predefined full model. In a dominance analysis, the higher the dominance score the more useful is the independent variable in predicting the response variable. We did not quantify the importance of each single variable, but rather the importance of the combined effect of summer and winter severity and ruggedness ("environmental variables") and human footprint and protected area coverage ("anthropogenic variables"). Thus, we fitted 3 models for each of the 11 species; a full model containing all variables, a model containing only the environmental variables and a model containing only the anthropogenic variables. For all models we computed the R^2_{glmm}, a modified version of the classic R^2 which is suitable for mixed models (Nakagawa & Schielzeth., 2013). We sampled 1,000 values from the posterior distribution of the model parameters and bootstrapped the R^2_{glmm} 1,000 times. We finally rescaled the dominance score for it to range from 0 to 100%.

2.3.3. Quantifying the effect of anthropogenic variables on the size of the species' niche

In another approach to assess the relative extent to which anthropogenic variables influence the realized niche of the studied large mammals we quantified the geographic representation of the environmental niche for each species (i.e. the potential suitable area available due to environmental predictors only; Guisan & Thuiller, 2005). We predicted the probability of a species' occurrence within a grid cell both when anthropogenic variables were set at their minimum value (i.e. we simulated a landscape free of all human influence: no human footprint and no protected areas) and when anthropogenic variables are set to their current values. We summed these predicted occurrences across Europe to estimate the expected number of occupied cells (i.e. the size of a species' suitable area in Europe). A sum of predictions in a human-free landscape higher than a sum of prediction for the full model implies that the species increase its range in absence of human influence in the landscape. We sampled 1,000 values from the posterior distribution of the model parameters and bootstrapped the niche area 10,000 times.

3. Results

For ease of interpretation we consider five disturbance levels (Venter et al., 2016). A 'no human disturbance' area has a human footprint of 0; a 'low disturbance' area a human footprint of 1-2; a ‘moderate disturbance’ area a human footprint of 3-5; a ‘high disturbance’ areas a human footprint of 6-11; and ‘very high disturbance’ area a human footprint of 12-50, following the definition by Venter et al. (2016).

With a median human footprint of 12.2, summary statistics show that more than 50% of Europe is considered to be an area of very high human disturbance, while less than 8% of Europe is considered to have no to low human footprint (Figure 1). Protected areas are spread throughout Europe with the median area of protected areas per 100 km^2 (i.e. per 10km x10 km grid cell) being 9 km^2 (Q1 = 0 km^2, Q3 = 41 km^2). Grid cells containing at least 50 km^2 of protected areas tended to have on average a slightly lower human footprint than grid cells containing less than 50km^2 of protected areas (median = 10.04 and 12.98 respectively).

The 7 large ungulates and 4 large carnivores studied demonstrate great variability regarding their presence across the human footprint gradient (Figure 2). Roe deer (median of 12.8, Q1 = 8.2, Q3 = 18.2) and wild boar are the species present at the highest human footprint (median = 13.5, Q1 = 9.2, Q3 = 18.7). These simple statistics show that more than 50% of the roe deer and wild boar distribution occurs in areas of very high human pressure. Wild reindeer (median = 3.9, Q1 = 2.1, Q3 = 4.8) and wolverines (median = 2.7, Q1 = 1.1, Q3 = 4.4) are at the other end of the spectrum with a distribution in places that are least impacted by human disturbance. Our data shows that wolves are not restricted to “wild” remote places but can live in areas where human disturbance is high (median = 9.6, Q1 = 6.8, Q3 = 13). More than 25% of their distribution is located in areas where human disturbance is very high.

Results from the dominance analysis show that the distributions of all 11 species are largely explained by the environmental variables (Figure 3). In fact, environmental variables consistently dominate the models (with a relative importance close to 100%) and the influence of anthropogenic variables in our models is shown to be close to 0% or even negative (i.e. the R^2 of the model gets worse as we include these variables). Only for red deer and wolf anthropogenic variables increase the models' R^2 values (median = 3.3% and median = 12% respectively), although their effects were still considerably lower than those of the environmental variables. Overall, our results show that the anthropogenic variables are poor predictors of species distribution compared to the other environmental variables.

Finally, in Figure 4 we show that anthropogenic variables hardly influence the area of species' distribution. The environmental niche for most studied mammals (i.e. ibex, wild reindeer, bears, wolverines, red deer and moose) is weakly influenced by setting both human footprint and protected areas to zero. Only in the case of chamois and roe deer did we observe a strong decrease of predicted suitable area when setting the anthropogenic variables to zero (median = -13,900 and -284,400 km^2 respectively). We also observed a decrease of the predicted suitable area for wolverine, wild reindeer and ibex when removing anthropogenic effects (median = -12,900 and -6,200 km^2 respectively), due to the removal of protected areas (see Figure S1 and S2 in the Annexes). In contrast, the total predicted suitable area available for wolf, lynx and wild boar increases when anthropogenic effects are set to zero (median = 50,700, 133,400 and 131,200 km^2 respectively). These predicted gains represent 17%, 6% and 4% of the actual lynx, wolf and wild boar distribution.

4. Discussion

In this study we have demonstrated that the large scale distributions of Europe's main large mammalian species include areas of high to very high human disturbance. Even though there is a wide distribution of high human disturbance combined with a rarity of remote places in the European landscape these results show that large mammals are able to maintain a presence in these heavily modified multi-use landscapes. We have further shown that human disturbance and protected area coverage are only minor drivers of large mammal distributions at the continental scale. For all large mammals, both anthropogenic variables are weak or negligible predictors of their distribution as opposed to environmental variables.

Large scale studies (e.g. with a continental scope) can produce results that apparently contradict finer scale studies (e.g. with a sub-national scope) and failure to consider scale can lead to misinterpretation of results (Johnson, 1980). Our results suggest that conservation scientists should be careful about the scale used to answer their research questions. While our models of first order habitat selection (distribution range) suggest that anthropogenic factors such as protected area coverage and human disturbance are at best minor drivers of large ungulate and large carnivore distribution in Europe, results should not be generalized to higher order habitat selection at finer scales. Indeed, many fine scale studies find that the presence or habitat use of large mammals is mainly negatively affected by proximity to human infrastructure such as roads or cities (for red and roe deer see D'Amico et al., 2016, Polfus et al., 2011 for moose, Lesmerises et al., 2013 for wolves; Gundersen et al., 2019 for wild reindeer; May et al., 2006 for wolverines and Pęksa & Ciach, 2018 for chamois), but also that one way of coping with this proximity is temporal rather than spatial segregation (e.g. animals become primarily night active, Gaynor et al., 2018). Different processes drive distributions at different scales, it is therefore not surprising that results will vary across studies at different scales. For instance, while mountain ungulates forage on steep slopes, human settlements are usually located in the valley bottoms, allowing a vertical coexistence in near proximity. Thus, topographic complexity can provide refuge areas that facilitate human wildlife proximity (Richard & Côté, 2016).

Similar to other large scale studies, our analysis is also limited to distributional data, which do not contain information about density, behavior or demography and which quality is highly variable and coarse. Therefore, while our results document the ability of populations of ungulates and carnivores to persist and use habitat in the general proximity to areas of high human footprint, this does not mean these species are not influenced by humans in other ways and at other spatio-temporal scales. Another challenge is the lack of historical distribution data which make inferences about causal relationships between human activities and land uses with changes in distributions and population of ungulates populations. While some attempts to reconstruct large mammals' historical distribution are made, they rely on current distribution (Belotte et al., 2020)

The low effect of anthropogenic variables in our models also implies a low effect of protected areas on large mammal distributions in Europe. This is in line with other studies on the distribution of large mammals (for ungulates see Linnell et al., 2020; for carnivores Chapron et al., 2014). Two main reasons are the small size of most European protected areas relative to spatial requirements of large mammals and the fact that although European protected areas have on average a lower human footprint they are not free of human disturbance. In fact, most European protected areas permit harvesting or culling of large herbivores as well as livestock grazing, extensive agriculture and forestry (Linnell et al., 2015) , and they encourage tourism. It should be noted that these disturbances are not captured by the Human Footprint Index which focuses on infrastructure, implying that the actual disturbance level of protected areas might in reality be higher than the ones used in this analysis. Only in the case of the wolverine and the wild reindeer does protected area coverage increase the suitable area available because their actual distribution is largely located within protected areas.

This demonstration of the weak effect of human footprint on species distribution compared to the effect of environmental covariates indicates that most of the large mammals included in our study are flexible enough to adapt to the dramatic anthropogenic impacts which have occurred in the European landscape during recent centuries. This is reflected by the overall generalist behavior of these species. For instance, moose seem to adapt to road presence and associated forage in their proximity (Eldegard et al., 2012), while agricultural landscapes help roe deer to supplement their diet (Abbas et al., 2011). In contrast, a species' tolerance to environmental factors (such as winter severity) obviously reflects physiological and phylogenetic constraints which respond much more slowly, if at all.

5. Conclusion

Our results contribute to advancing the science of human-wildlife coexistence in heavily modified landscapes. Although several papers rightly point out that large mammals are threatened by human impacts in many parts of the world (Ripple et al., 2014; Ripple et al., 2015) we argue that the European experience demonstrates that coexistence between humans and wild large mammals at broad scales and continental scale recovery is possible. The high impacts that Europe's dense populations have on the continent's natural habitats make it impossible for nature conservation authorities to rely on a land-sparing policy for large mammals because protected areas large enough to support viable populations of these space demanding species don't exist. Our results show that large mammals are able to adapt to the modern European anthropogenic landscape to a surprising degree. Ultimately, the challenge of coexistence seems to not so much be about whether species are able to cope with human disturbance but whether humans are willing to share their landscape and host wildlife in their backyards (Title & Bemmel, 2018).

6. Data availability statement

To make our study reproducible we have made the dataset and scripts available at the DOI link: DOI 10.17605/OSF.IO/XV8NH. For access to the raw data concerning large ungulates distribution please refer to the DOI link: DOI 10.17605/OSF.IO/N5P2U.

7. Acknowledgments

This study was funded by the Research Council of Norway (grant number 251112) and a PhD scholarship to BC from the Norwegian University of Science and Technology.

8. References

Abbas, F., Morellet, N., Hewison, A. M., Merlet, J., Cargnelutti, B., Lourtet, B., ... & Verheyden, H. (2011). Landscape fragmentation generates spatial variation of diet composition and quality in a generalist herbivore. *Oecologia*, *167*(2), 401-411.

Alexander, J. S., Gopalaswamy, A. M., Shi, K., Hughes, J., & Riordan, P. (2016). Patterns of snow leopard site use in an increasingly human-dominated landscape. *PLoS One*, *11*(5).

Apollonio, M., Andersen, R., & Putman, R. (Eds.). (2010). *European ungulates and their management in the 21st century*. Cambridge University Press.

Azen, R., & Budescu, D. V. (2003). The dominance analysis approach for comparing predictors in multiple regression. *Psychological methods*, *8*(2), 129.

Beguin, J., Martino, S., Rue, H., & Cumming, S. G. (2012). Hierarchical analysis of spatially autocorrelated ecological data using integrated nested Laplace approximation. *Methods in Ecology and*

Evolution, *3*(5), 921-929.

Belote, R. T., Faurby, S., Brennan, A., Carter, N. H., Dietz, M. S., Hahn, B., ... & Gage, J. Mammal species composition reveals new insights into Earth's remaining wilderness. *Frontiers in Ecology and the Environment*.Carter, N. H., & Linnell, J. D. (2016). Co-adaptation is key to coexisting with large carnivores. *Trends in Ecology & Evolution*, *31*(8), 575-578.

Carter, N. H., Shrestha, B. K., Karki, J. B., Pradhan, N. M. B., & Liu, J. (2012). Coexistence between wildlife and humans at fine spatial scales. *Proceedings of the National Academy of Sciences*, *109*(38), 15360-15365.

Chapron, G., Kaczensky, P., Linnell, J. D., von Arx, M., Huber, D., Andrén, H., ... & Balčiauskas, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *science*, *346*(6216), 1517-1519.

Cretois, B., Linnell, J. D., Kaltenborn, B. P., & Trouwborst, A. (2019). What form of human-wildlife coexistence is mandated by legislation? A comparative analysis of international and national instruments. *Biodiversity and Conservation*, *28*(7), 1729-1741.

D'Amico, M., Périquet, S., Román, J., & Revilla, E. (2016). Road avoidance responses determine the impact of heterogeneous road networks at a regional scale. *Journal of Applied Ecology*, *53*(1), 181-190.

Díaz, S., Settele, J., Brondízio, E., Ngo, H., Guèze, M., Agard, J., ... & Chan, K. (2020). Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.

Dietz, A. J., Kuenzer, C., & Dech, S. (2015). Global SnowPack: a new set of snow cover parameters for studying status and dynamics of the planetary snow cover extent. *Remote Sensing Letters*, *6*(11), 844-853.

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., ... & Münkemüller, T. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*(1), 27-46.

Eldegard, K., Lyngved, J. T., & Hjeljord, O. (2012). Coping in a human-dominated landscape: trade-off between foraging and keeping away from roads by moose (Alces alces). *European journal of wildlife research*, *58*(6), 969-979.

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, *360*(6394), 1232-1235.

Guisan, A., & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology letters*, *8*(9), 993-1009.

Gundersen, V., Vistad, O. I., Panzacchi, M., Strand, O., & van Moorter, B. (2019). Large-scale segregation of tourists and wild reindeer in three Norwegian national parks: Management implications. *Tourism Management*, *75*, 22-33.

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, *61*(1), 65-71.

Leblond, M., Dussault, C., & Ouellet, J. P. (2010). What drives fine-scale movements of large herbivores? A case study using moose. *Ecography*, *33*(6), 1102-1112.

Lesmerises, F., Dussault, C., & St-Laurent, M. H. (2013). Major roadwork impacts the space use behaviour of gray wolf. *Landscape and urban planning*, *112*, 18-25.

Lindgren, F., & Rue, H. (2015). Bayesian spatial modelling with R-INLA. *Journal of Statistical*

Software, *63*(19), 1-25.

Linnell, J. D., Cretois, B., Nilsen, E. B., Rolandsen, C. M., Solberg, E. J., Veiberg, V., ... & Kaltenborn, B. (2020). The challenges and opportunities of coexisting with wild ungulates in the human-dominated landscapes of Europe's Anthropocene. *Biological Conservation*, *244*, 108500.

Linnell, J. D., Kaczensky, P., Wotschikowsky, U., Lescureux, N., & Boitani, L. (2015). Framing the relationship between people and nature in the context of European conservation. *Conservation Biology*, *29*(4), 978-985.

Linnell, J. D. C., & Zachos, F. E. (2010). Status and distribution patterns of European ungulates: genetics, population history and conservation. *Ungulate management in Europe: problems and practices*, 12-53.

May, R., Landa, A., van Dijk, J., Linnell, J. D., & Andersen, R. (2006). Impact of infrastructure on habitat selection of wolverines Gulo gulo. *Wildlife Biology*, *12*(3), 285-295.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in ecology and evolution*, *4*(2), 133-142.

Nellemann, C., Støen, O. G., Kindberg, J., Swenson, J. E., Vistnes, I., Ericsson, G., ... & Ordiz, A. (2007). Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. *Biological Conservation*, *138*(1-2), 157-165.

Pęksa, Ł., & Ciach, M. (2018). Daytime activity budget of an alpine ungulate (Tatra chamois Rupicapra rupicapra tatrica): influence of herd size, sex, weather and human disturbance. *Mammal Research*, *63*(4), 443-453.

Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., ... & Sexton, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, *344*(6187), 1246752.

Polfus, J. L., Hebblewhite, M., & Heinemeyer, K. (2011). Identifying indirect habitat loss and avoidance of human infrastructure by northern mountain woodland caribou. *Biological Conservation*, *144*(11), 2637-2646.

Redpath, S. M., Young, J., Evely, A., Adams, W. M., Sutherland, W. J., Whitehouse, A., ... & Gutierrez, R. J. (2013). Understanding and managing conservation conflicts. *Trends in ecology & evolution*, *28*(2), 100-109.

Richard, J. H., & Côté, S. D. (2016). Space use analyses suggest avoidance of a ski area by mountain goats. *The Journal of Wildlife Management*, *80*(3), 387-395.

Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., ... & Macdonald, D. W. (2015). Collapse of the world's largest herbivores. *Science advances*, *1*(4), e1400103.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., ... & Schmitz, O. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*(6167), 1241484.

Svenning, J. C., Fløjgaard, C., & Baselga, A. (2011). Climate, history and neutrality as drivers of mammal beta diversity in Europe: insights from multiscale deconstruction. *Journal of Animal ecology*, *80*(2), 393-402.

Tattersall, G. J., Sinclair, B. J., Withers, P. C., Fields, P. A., Seebacher, F., Cooper, C. E., & Maloney, S. K. (2012). Coping with thermal challenges: physiological adaptations to environmental temperatures. *Comprehensive Physiology*, *2*(3), 2151-2202.

Title, P. O., & Bemmels, J. B. (2018). ENVIREM: an expanded set of bioclimatic and topographic variables increases flexibility and improves performance of ecological niche modeling. *Ecography*, *41*(2), 291-307.

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Van Moorter, B., Alberts, S. C., ... & Bartlam-Brooks, H. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, *359*(6374), 466-469.

Venter, O., Sanderson, E. W., Magrach, A., Allan, J. R., Beher, J., Jones, K. R., ... & Levy, M. A. (2016). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature communications*, *7*(1), 1-11.

Figure 1: Map of the distribution of human disturbance level in our study area

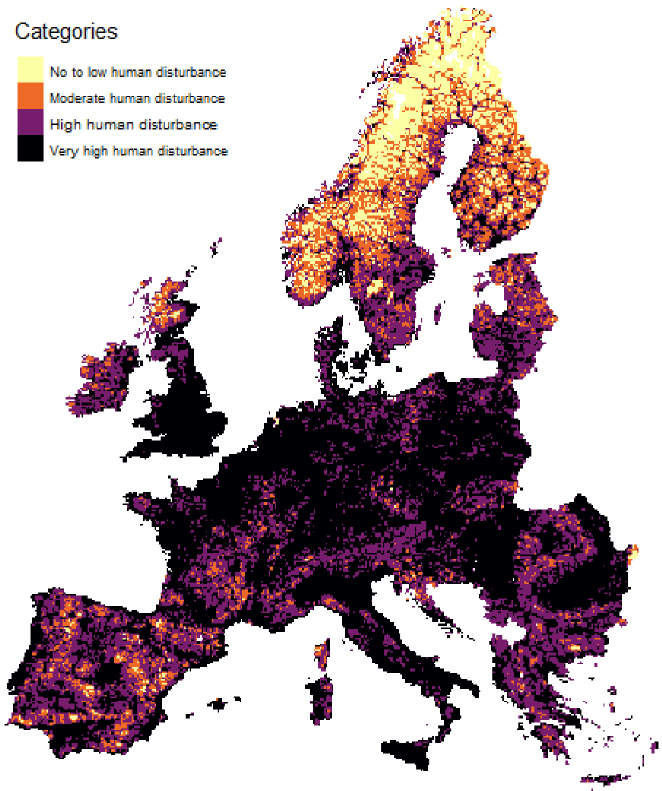

Figure 2: Species' distributions across the human footprint gradient. From top to bottom: roe deer, red deer, moose, wild reindeer, chamois, ibex, wolf, lynx, bear, wolverine, and the European human footprint distribution.

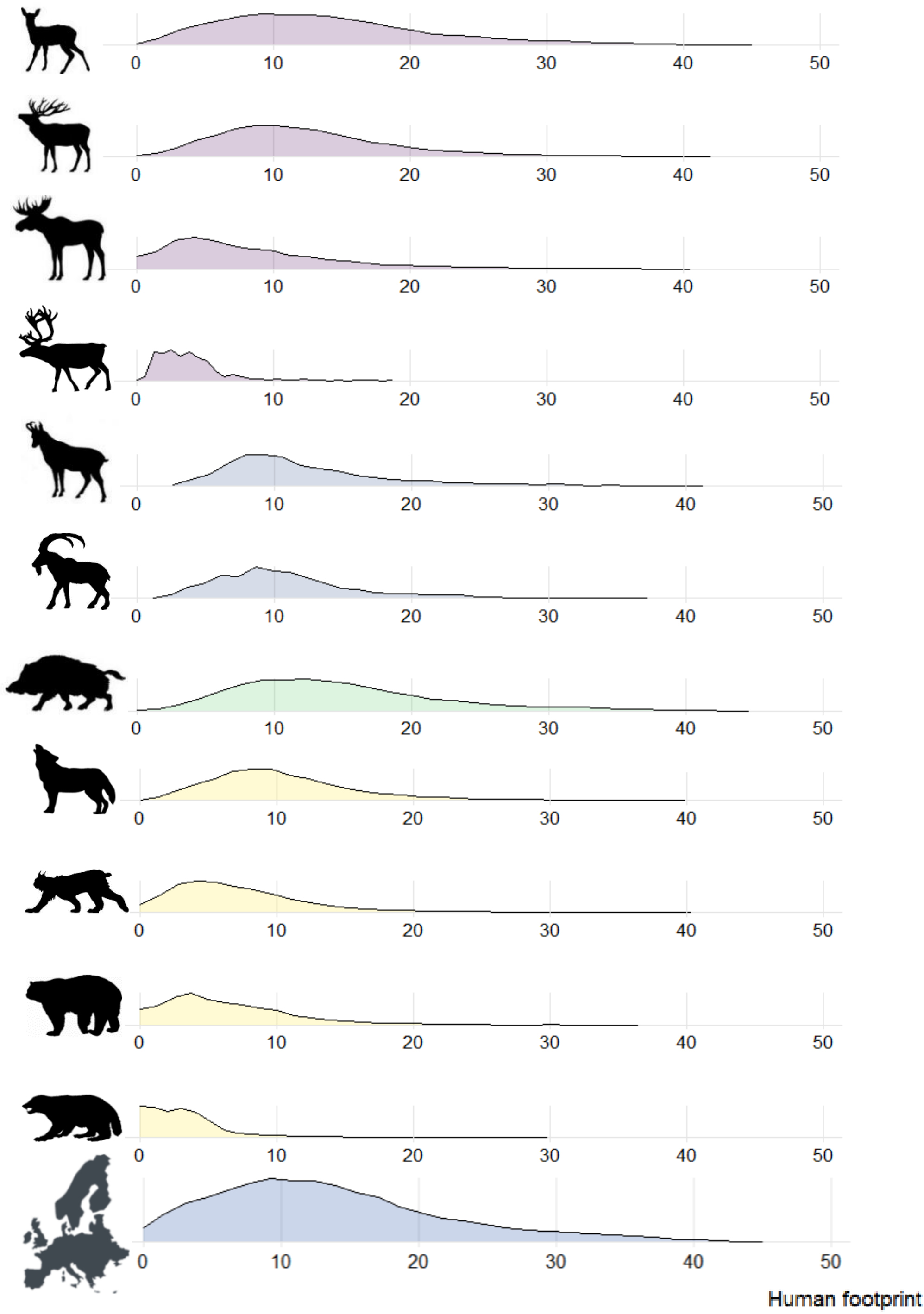

Figure 3: Relative importance for model fit (in percentage) of anthropogenic variables (human footprint and protected area coverage; in red) and environmental variables (winter and summer severity and terrain ruggedness; in green) to species distribution. Negative importance indicates a drop in the R^2 when the variable is included in the model. Points represent the median value, thick lines the 50% credible interval and thin lines the 95% credible interval.

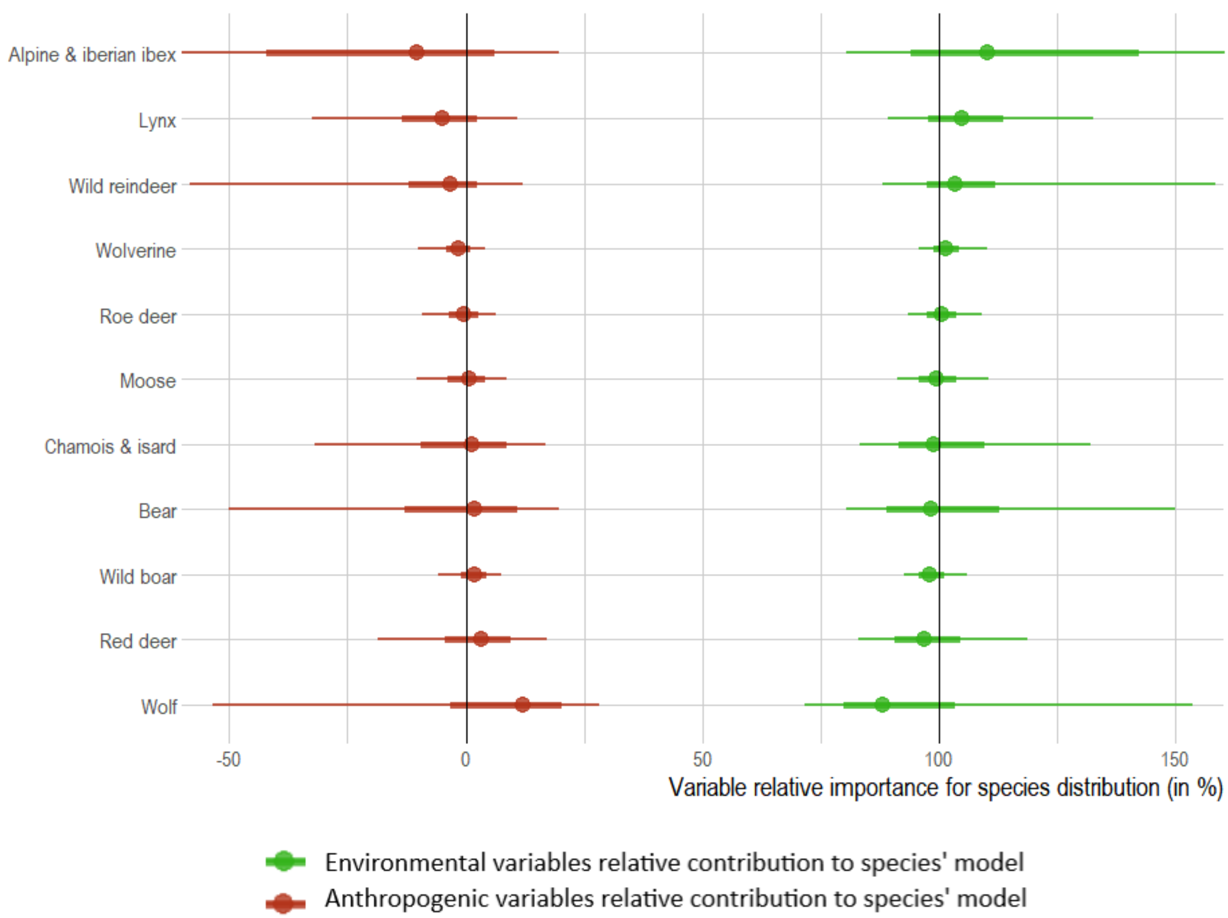

Figure 4: Predicted environmental niche of European large mammals in presence (y axis) and absence (x axis) of anthropogenic variables in km². A value below the iso-line indicates an increase in potentially suitable area when removing anthropogenic variables. Thin lines represent the 95% credible interval.