Walking on the dark side: Anthropogenic factors limit suitable habitat for gray wolf (*Canis lupus*) in a large natural area covering Belarus and Ukraine

Svitlana Kudrenko [a,b,c,1,*], Viktar Fenchuk [a], Julien Vollering [d],
Andreas Zedrosser [c,e], Nuria Selva [f,g], Katarzyna Ostapowicz [h], James C. Beasley [i,j],
Marco Heurich [b,k,l]

[a] *Frankfurt Zoological Society, Bernhard Grzimek Allee 1, 60316 Frankfurt, Germany*
[b] *Faculty of Environment and Natural Resources, University of Freiburg, Germany*
[c] *Faculty of Technology, Natural Sciences and Maritime Sciences, Department of Natural Sciences and Environmental Health, University of South-Eastern Norway, Gullbringvegen 36, 3800 Bø, Norway*
[d] *Department of Environmental Sciences, Western Norway University of Applied Sciences, Sogndal, Norway*
[e] *Department for Integrative Biology, Institute for Wildlife Biology and Game Management, University for Natural Resources and Life Sciences, Gregor Mendel Str. 33, A-1180 Vienna, Ausrtia*
[f] *Institute of Nature Conservation, Polish Academy of Sciences, Mickiewicza 33, 31-120 Krakow, Poland*
[g] *Departamento de Ciencias Integradas, Facultad de Ciencias Experimentales, Centro de Estudios Avanzados en Física, Matemáticas y Computación, Universidad de Huelva, 21071 Huelva, Spain*
[h] *Norwegian Institute for Nature Research (NINA), FRAM – High North Centre from Climate and the Environment, Tromsø 9296, Norway*
[i] *Savannah River Ecology Laboratory, University of Georgia, Aiken, SC, USA*
[j] *Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA, USA*
[k] *Bavarian Forest National Park, Grafenau, Germany*
[l] *Institute for Forest and Wildlife Management, Inland Norway University of Applied Science, Koppang, Norway*

ARTICLE INFO

ABSTRACT

Due to successful conservation initiatives and legislations, the grey wolf (Canis lupus) is re-colonising its historic range in Europe. However, wolves have never been extirpated across large areas in Eastern Europe but are often constrained to remote and inaccessible places due to centuries of persecution. This study aimed to identify the potentially suitable wolf habitats in Polesia, a massive cross-border lowland region extending over southern Belarus and northern Ukraine, which are often neglected in large carnivore studies at the continental scale. We hypothesized that anthropogenic rather than environmental factors govern wolf habitat suitability. We used a dataset of 4191 GPS locations obtained from radio-collared wolves (n = 26) and confirmed observations (n = 231) during 2014–2021 and applied maximum entropy method to estimate relative habitat suitability for wolves in Polesia. Artificial light at night (ALAN), pro-portion of cropland and tree cover were the most important factors affecting wolf habitat suit-ability. Road densities contributed poorly to predicting habitat suitability for wolves. Our models predicted a quarter of Polesia as suitable habitat and revealed priority areas connecting the important source populations in the Chornobyl Exclusion Zone in the east and the Białowieża Forest in the west and thus essential for long-term wolf conservation. Our results provide the

* Corresponding author at: Frankfurt Zoological Society, Bernhard Grzimek Allee 1, 60316 Frankfurt, Germany.
E-mail address: svitlana.kudrenko@fzs.org (S. Kudrenko).
[1] ORCID iD: 0000–0001-9532–4873

bases for effective, long-term wolf monitoring and management programs in both Belarus and Ukraine. However, national and transboundary wolf management in Polesia has been extremely challenging since 2022 due to the ongoing war and subsequent habitat degradation in this part of Europe.

1. Introduction

Accelerating habitat loss and degradation caused by direct or indirect human activities threaten biodiversity and ecosystem functions worldwide (Schipper et al., 2008). Habitat fragmentation reduces species diversity and abundance and can imperil the long-term viability of isolated populations, intensifying their vulnerability to local extinctions and inbreeding depression (Crooks et al., 2011). Wilderness areas shrink and stop providing ecosystem services because of resource extraction, conversion of natural landscapes to cropland, urban sprawl and road development (Maxwell et al., 2016). Continuing cropland expansion and land-use intensification are major drivers of terrestrial biodiversity loss (Kehoe et al., 2017). Growing concerns about the negative effects of artificial light at night (ALAN) signal that it might have an additional pervasive impact on wildlife (Longcore and Rich, 2004; Cieraad et al., 2023). ALAN further degrades a wide range of ecosystems, from urban to remote wilderness areas, as fewer than 1/5 of Key Biodiversity Areas worldwide remain entirely unpolluted by ALAN (Gaston et al., 2021).

Terrestrial mammals avoid degraded sites that no longer provide sufficient refuge, forage quality or wild prey base (Wolf and Ripple, 2017). Large carnivores are particularly sensitive to habitat loss and fragmentation owing to their biological traits, slow reproduction rate and susceptibility to poaching (Enserink and Vogel, 2006). Large carnivores exhibit avoidance of anthropogenic development and their abundances in degraded habitats are lower than in natural landscapes (Whittington et al., 2022). Many large carnivores have been persecuted for centuries and eradicated within their former distribution (Ripple et al., 2014). Consequently, most species are now limited to clustered populations or have been extirpated within their historical range (Enserink and Vogel, 2011). Loss of large carnivores can trigger cascading effects such as disrupting biogeochemical cycles and changes in vegetation patterns (Estes et al., 2011; Ritchie et al., 2012). Protected areas often contain high-quality habitats patches preferred by these species, yet large carnivores rarely restrict their home range to the borders of protected areas and can travel extensively during dispersal and re-colonize habitats that have become suitable (Wabakken et al., 2007; Byrne et al., 2018).

Grey wolves (*Canis lupus*) demonstrate high ecological resilience towards landscape heterogeneity unless persecution by people is high (Fritts et al., 2003). Wolves can benefit from increasing human tolerance and favourable conservation policies, demonstrating adaptability towards landscape modifications and permanent human presence (Chapron et al., 2014). Nonetheless, studies on wolves' habitat concluded that the availability of suitable habitat was not the only factor that limited species expansion (Jędrzejewski et al., 2008; Huck et al., 2011; Nowak et al., 2017). Wolves minimized their presence in areas with high densities of humans and main roads which might be linked to anthropogenic mortality (Kabir et al., 2017; Simpson et al., 2023).

Studies on wolves are often biased toward developed countries and particular "blind spots" are Belarus and Ukraine, which to date have largely been neglected in pan-European carnivore studies (Boitani and Linnell, 2015; Cimatti et al., 2021). This region's lack of systematic monitoring and published robust data leads to substantial uncertainty about wolf distributions, densities and how different landscape features affect their habitat use, movements and dispersal (Boitani et al., 2018; Cherepanyn et al., 2023). Wolf populations in Polesia, a lowland region covering southern Belarus and northern Ukraine, are of particular conservation importance, because they link wolf populations in the Russian Federation with populations in Poland and the Baltic states. However, wolf's long-term viability in these countries remains uncertain. The wolf remained a widespread species in Belarus and Ukraine until the mid-20th century. After WWII, wolves were considered a vermin species posing a severe threat to economic prosperity in areas important for livestock breeding and human safety (injurious attacks on humans and disease transmission) and thus thousands of wolves were systematically eradicated (Shkvyrya et al., 2014). In Polesia, overhunting accompanied by habitat degradation – mire drainage, road and irrigation system constructions, building the Chornobyl nuclear power plant and related infrastructure – were causing the decline in population numbers and species range contraction that potentially altered wolf breeding, pack and population structures (Sidorovich, 2011). After decades of government-sponsored persecution, wolves are still hunted in Belarus and Ukraine. Hunting is deficiently regulated; thus, wolves are hunted year round and permanent wolf presence was reported mainly within regional protected areas (Deryabina et al., 2015; Niedziałkowski et al., 2022), yet poaching there may limit species proliferation and population growth (Shkvyria and Vishnevskiy, 2012). Therefore, we suspect that the species does not realize its full potential distribution in Polesia.

Our main goal is to assess the influence of anthropogenic development on habitat suitability for wolves and quantify the extent of their suitable habitat in Polesia. Developing habitat suitability models at the home range level can provide information on biotic and anthropogenic variables shaping the species' distribution and allow predicting habitat suitability for areas where species occurrences have not yet been recorded (Guisan et al., 2017). To date, no habitat studies have been conducted at a fine spatial scale for the region and habitat suitability assessment is needed for guiding conservation measures. Assessing the habitat suitability in Polesia will greatly improve our understanding of the status of wolves in Eastern Europe and the long-term viability of populations on the continental scale (Redpath et al., 2013). The main objectives of this study are 1) to identify which landscape features and anthropogenic factors delineate suitable wolf habitat in the Polesia region, 2) to evaluate the role of regional protected areas in wolf conservation, and 3) to identify areas of interest for large carnivore conservation. We predict higher probability of wolf presence in areas with a) less intense artificial light at night, b) lower human and road densities; c) lower proportion of cropland; d) less modified land cover types and e) high overlap with protected areas.

2. Material and methods

2.1. Study area

Polesia (~164 500 km²) is a lowland geographical and historical region in the temperate zone of the East European Plain in northern Ukraine and southern Belarus (Fig. 1). The average altitude is 120–150 m above sea level. The area is comprised mainly of croplands (46%), coniferous (23%), and broadleaved (11%) forests, and to a lesser extent of mixed forests, grasslands, wetlands, and urban areas (Table A1). Polesia has a dense network of lakes and rivers that repeatedly flood throughout the year (maximum submergence in late March-early April) (Marynych et al., 1985). The climate is continental with mean temperatures from − 4 to − 7°C in January and from + 18 to + 19°C in July. The mean annual precipitation is 550–650 mm. The area is heavily modified by human activities such as logging with subsequent afforestation of monocultures (dominant tree species are Scots pine (*Pinus sylvestris*), European oak (*Quercus robur*), birch (*Betula* spp.)), wetland drainages, livestock grazing and amber mining. The first protected areas in Polesia, the Belarusian part of the Białowieża Forest (1 501 km²) and the Poliskyi Nature Reserve (201 km²) in Ukraine, were established in 1932 and 1968, respectively. Additional protected areas were later established, including the Chornobyl Exclusion Zone (hereafter CEZ), a ~4 300-km² area abandoned after the catastrophe at the Chornobyl nuclear power plant in April 1986 (Beresford and Copplestone, 2011). According to IUCN conservation classifications, legally protected areas covered ~22 000 km² (13.3%) of Polesia in 2021.

The mammalian fauna of Polesia is diverse and includes three large carnivore species, the brown bear (*Ursus arctos*), Eurasian lynx (*Lynx lynx*), both protected, and the grey wolf, which can be hunted year-round (Shkvyria and Vishnevskiy, 2012). The main ungulate species are roe deer (*Capreolus capreolus*), wild boar, (*Sus scrofa*), and moose (*Alces alces*) (protected) (SSC, 2020; Mindovkillya, 2021). Red deer (*Cervus elaphus*) are permanently present only in the CEZ and some surrounding areas in the eastern part of Polesia (S. Zhyla, S. Kudrenko, unpublished data). Despite the conservation success, European bison (*Bison bonasus*) free-ranging herds in Polesia are limited to the Białowieża Forest and CEZ (Belarus) due to forest fragmentation and human disturbance (Gashchak et al., 2017). All ungulate species are hunted during the established season, except the moose and bison, which are red-listed species in Ukraine and Belarus (only bison).

2.2. Wolf data and environmental variables

We compiled wolf presence data for the period 2014–2021 from various sources: (1) telemetry data from 26 radio-collared wolves in the Białowieża Forest, central Polesia and the CEZ (123 426 GPS locations); (2) remote camera-trapping studies in the Białowieża Forest (n = 65 observations) and eastern Polesia (n = 44); (3) scat samples confirmed by genetic analyses in eastern and central
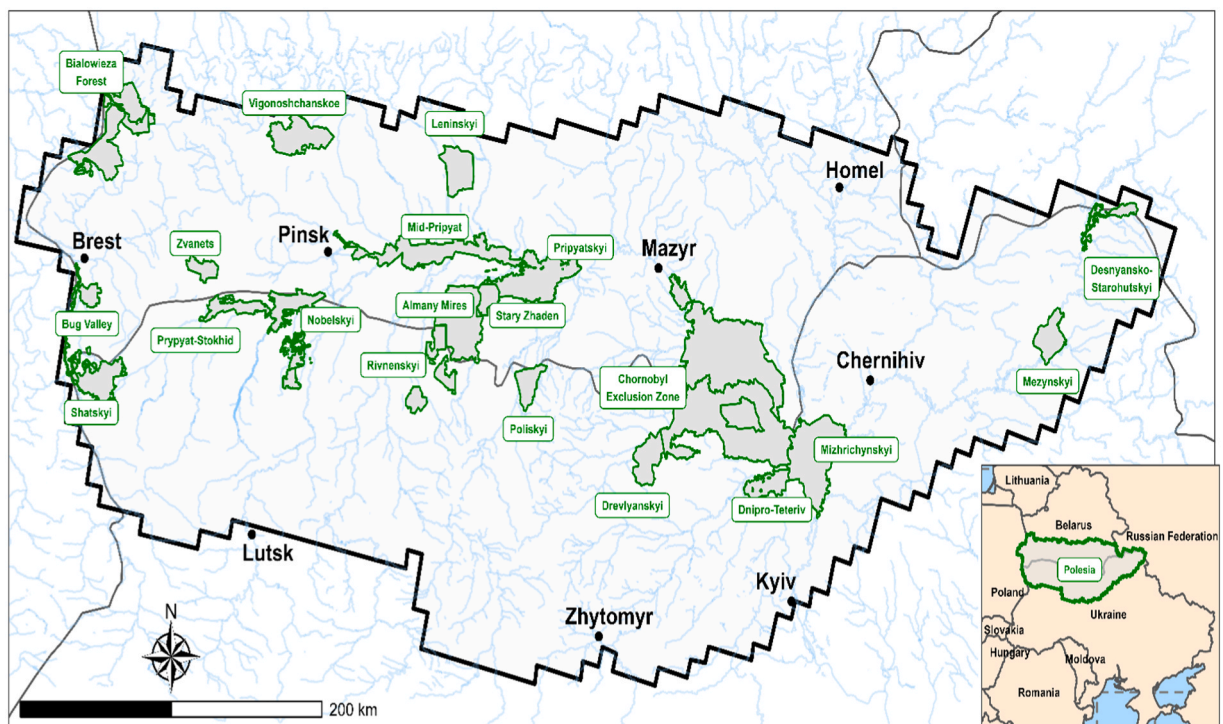

Fig. 1. Study area of Polesia. Masked areas indicate protected areas (>100 km²) across the region in 2021.

Polesia (n = 61 scats); (4) geo-referenced wolf records (n = 61), i.e. photos, remote camera records and other confirmed observations (tracks and scats) from the Ukrainian Biodiversity Information Network database (UkrBIN, 2017). For telemetry studies, all wolves were captured with foothold traps (Minnesota Brand, Minnesota Trapline Products, MN, USA), sedated with a 0.1% solution of medetomidine at 1 ml/10 kg (the Białowieża Forest, central Polesia) and 0.06 mg/kg(the CEZ), hobbled and muzzled. Solution of 0.5% atipamezole was injected as an antidote in the Białowieża Forest and central Polesia. Capture-related minor injuries, if occurred, were disinfected, bandaged and animals were treated with antibiotics. All wolves were fitted with GPS collars with an automatic drop-off mechanism (VECTRONIC Aerospace GmbH, Berlin, Germany). We programmed collars to collect a GPS location every hour (n = 7, the Białowieża Forest and central Polesia in October-November 2017); every 3 h (n = 5, the Białowieża Forest) and every 35 min (n = 14, the CEZ)). Collared wolves were released at the capture location following collar attachment and processing. Animal capture and handling procedures and monitoring protocols were approved and permitted by local authorities and research institutions in Belarus. Wolf capture and handling in the Belarusian CEZ was carried out in accordance with the University of Georgia Animal Care and Use protocol A2015 05–004-Y2-A1.

Camera traps were deployed in the Belarusian part of the Białowieża Forest opportunistically during the period January 2014-December 2017 (27 locations). In the Ukrainian CEZ, camera traps were deployed every second grid cell (2.5 ×2.5 km) with a minimum distance among neighbouring camera trap locations of at least 1 km and were active between November 2020-March 2021 (68 locations), whereas in the western part of the CEZ and six protected areas (PAs) across Polesia in Ukraine camera traps were randomly distributed in 2021 at the central points of every second grid cell (3.1 ×3.1 km) unless the central points were not reachable or located in human-inhabited area (89 locations) following Fiderer et al. (2021). All camera traps were unbaited, kept active throughout a 24-h cycle at given locations for a minimum of two months and programmed to take consecutive images when triggered. All genetic samples were collected opportunistically while conducting wolf research in Belarus (2013–2017) and Ukraine (2020–2021).

We used a resolution of 1 km with the projection ETRS89-extended/LAEA Europe (EPSG:3035), aligned with the 10 km resolution grid from similar studies on European large carnivores (Chapron et al., 2014; Cimatti et al., 2014). In 75% of 1 km^2 grid cells with recorded wolf presence in Polesia, wolf presence was detected more than once. To reduce inaccuracy in model projections associated with spatial autocorrelation (Grilo et al., 2019), we discarded duplicates within cells, resulting in 4191 presences.

To predict suitable wolf habitat, we considered a set of environmental variables based on previous studies and data availability (see Table 1) (Jędrzejewski et al., 2008; Kabir et al., 2017; Grilo et al., 2018). All environmental variables were geo-referenced, re-sampled and clipped to the same geographical extent with a cell size of 1 km^2 (~30″). We used three variables related to land cover in the study area: (1) land cover type, (2) tree cover, and (3) normalized difference vegetation index (NDVI). Land cover data were retrieved from the European Space Agency Climate Change Initiative Land Cover (ESA CCI-LC) project (ESA, 2015). The seventeen land cover types (ESA, 2015) present in the study area were aggregated into five categories due to the species high adaptability to a wide range of habitats (Ballard et al., 2003): 1) open areas (56.5%), 2) forests (40%), 3) wetlands (1%), 4) urban areas (1.5%), and 5) water bodies (1%) (Table A2). We then calculated the dominant land cover type for each cell in the study area. We took as our tree cover variable the mean tree cover in a grid cell based on the canopy percentage per pixel during the peak of the growing season (Hansen et al., 2013). Data on ungulate diversity, distribution or density estimates were either not available or of too poor quality to include as predictive variables (Hundertmark, 2016; Lovari et al., 2018). Therefore, we used Moderate Resolution Imaging Spectroradiometer (MODIS) NDVI data as a proxy for ungulate presence because primary production positively affects herbivore abundance (Stoner et al., 2018). Monthly NDVI values from April and October were compiled from the National Aeronautics and Space Administration (NASA) website (Didan, 2015) to generate an interannual average estimate for the growing season during the study period.

We also considered a set of variables that more directly reflect anthropogenic impact: cropland, artificial light at night (ALAN),

Table 1
Trail of forward selection of explanatory variables in the best model under the optimal significance threshold of alpha = 0.05. Round – the round of explanatory variables' selection; variables – names of the explanatory variables included in the model; m – derived variables in the model; Dsq – the fraction of deviance explained; F – the F-statistic for the nested model comparison; df_e – degrees of freedom associated with explained deviance; df_u – degrees of freedom associated with unexplained deviance; p – the p-value for the F-statistic under the specified degrees of freedom.

Round	Variables	m	Dsq	F	df_e	df_u	p
1	artificial light	1	0.018	459.882	1	24997	0.00e+ 00
1	cropland	3	0.022	186.799	3	24995	0.00e+ 00
1	tree cover	5	0.017	86.855	5	24993	0.00e+ 00
1	landcover	4	0.012	76.161	4	24994	0.00e+ 00
1	tertiary roads	1	0.002	48.972	1	24997	2.66e-12
1	main roads	1	0.001	34.724	1	24997	3.85e-09
2	artificial light + cropland	4	0.025	60.512	3	24994	0.00e+ 00
2	artificial light + tree cover	6	0.021	14.266	5	24992	5.67e-14
2	artificial light + land cover	5	0.020	14.282	4	24993	1.20e-11
2	artificial light + main roads	2	0.018	7.167	1	24996	7.43e-03
2	artificial light + tertiary roads	2	0.018	6.153	1	24996	1.31e-02
3	artificial light + cropland + tree cover	9	0.028	13.417	5	24989	4.31e-13
3	artificial light + cropland + land cover	8	0.027	14.798	4	24990	4.43e-12
3	artificial light + cropland + main roads	5	0.025	4.020	1	24993	4.50e-02
3	artificial light + cropland + tertiary roads	5	0.025	1.095	1	24993	2.95e-01
4	artificial light + cropland + tree cover + land cover	13	0.029	10.841	4	24985	8.85e-09
4	artificial light + cropland + treecover + main roads	10	0.028	3.445	1	24988	6.35e-02

human density and road density. Cropland was defined as land cultivated for annual and perennial herbaceous crops for direct or indirect (forage and biofuel) human consumption. Original cropland data for a four-year interval 2016–2019 had higher resolution (30 m) than ESA CCI-LC (Potapov et al., 2021) and its pixel values (0 – no croplands or no data; 1 – croplands) were re-calculated by determining the mean value within the grid cells. Both human density (WorldPop, 2022a, 2022b) and artificial light at night (ALAN) are proxies for the level of human presence (Duffy et al., 2015; Cimatti et al., 2021). NASA's Black Marble nighttime lights product suite had values ranging from 0 (no artificial light at night emissions in a cell) to 255 (brightly-lit cell) (NASA, 2017). ALAN values were corrected for atmospheric, bidirectional reflectance distribution and seasonal effects (Román et al., 2018). The density of main (primary, secondary) and tertiary roads was considered a proxy for accessibility. We generated road variables by calculating the length of main and tertiary roads per gird cell using the QGIS Sum Line Length function based on Open Street Map data available via QGIS plugin (Trimaille, 2022). A protected area layer was available from the Protected Planet database (UNEP-WCMC and IUCN, 2022). We classified grid cells as those within protected areas (at least 50% of a cell covered by a protected area) and outside the protected areas (< 50% of a grid cell covered by a protected area).

2.3. Statistical analyses

We calculated means and standard deviations for all wolf presences and background points. To model the suitable habitat for wolves in Polesia, we analysed the spatial association between species records with environmental data using the *MIAmaxent* R package (Vollering et al., 2019) which implements a maximum-likelihood interpretation of the popular habitat suitability modelling software *Maxent* (Halvorsen et al., 2015). Following the principle of maximum entropy, this method fits models of a species' distribution that are as close as possible to uniform in space, while still satisfying constraints set by the recorded presences (Merow et al., 2013).

Wolf absence data had a higher degree of uncertainty than wolf presence data. Therefore, we based our analyses on presence-only data (Kabir et al., 2017). To facilitate presence-only modelling and to capture the range of variation in environmental variables over a large study area, we randomly sampled 25,000 background points for model training. We pre-screened the explanatory variables with a correlation test (Fig. B1) and selected only one variable from pairs with Pearson's correlation r > 0.7 (Dormann et al., 2013). We compared the performance of two highly correlated variables in one-variable models and included one variable in further modelling based on the AUC value. Consequently, we discarded NDVI in favour of tree cover (r = 0.72) and artificial light in favour of human density (r = 0.77). We then performed variable selection on the remaining candidate variables with the *MIAmaxent* package, under a range of significance thresholds (alpha = 0.05; 0.01; $1e^{-3}$; $1e^{-6}$; $1e^{-9}$) to increase the likelihood of identifying a model with an optimal level of complexity – one that is neither underfitted nor overfitted (Merow et al., 2013). The variable selection procedure in *MIAmaxent* first transforms explanatory variables into a set of derived variables which may better capture a species' response to the explanatory variables and then performs a stepwise forward selection of variables. We assessed the models' performance by measuring the area under the curve (AUC) of the receiver operating characteristic (ROC) curve calculated on an evaluation dataset, which was spatially separated from the locations used for model training (Wenger and Olden, 2012). The evaluation dataset was created by spatially subsetting 20% of wolf presences (n = 838, all from the CEZ) and an equal number of background points (n = 838) (Vollering et al., 2019). Models with AUC> 0.7 were considered to have a fair discriminative power (Elith et al., 2011).

To quantify wolf habitat, we converted the continuous relative habitat suitability index from the habitat suitability model into ordinal results (Merow et al., 2013). We identified values of the habitat suitability index found at the 25th, 50th and 75th percentiles of training presences to assess thresholds between habitat predicted as more or less suitable for wolf presence. Accordingly, we classified the values of the relative habitat suitability into four categories – very low (HSI<0.25), low (0.25 <HSI<0.5), high (0.5 <HSI<0.75) and very high (HSI>0.75) – by splitting the continuous gradient of suitability with quartile values (Recio et al., 2018). We reclassified the continuous habitat suitability predictions into few categories to facilitate interpretation of results and decision-making in wildlife management (Hirzel et al., 2006). For comparing potential and actual wolf distribution in protected areas, we calculated the area of suitable habitat patches (categories "high" and "very high") in protected areas > 100 km^2.

All calculations, variable transformations and data visualization were conducted in QGIS (QGIS.org, 2022) and using R packages *corrplot, dismo, dplyr, fasterize, fields, ggnewscale, ggplot2, ggpubr, ggspatial, ggrepel, maptools, raster, rgdal, rnaturalearth, sf* and *sp* (R Core Team, 2020).

3. Results

Univariate statistics indicated that cells with wolf presence significantly differed from cells without registered wolf presence (Table A3). Cells with wolf presence had lower ALAN values and lower proportion of cropland than cells where wolves were not recorded. Maximum human density in cells with wolf presence did not exceed 19.4 inhabitants/km^2. Tree cover percentage and NDVI values were higher and roads densities were lower in cells with recorded wolf presence. In addition, wolf observations were more common in cells with forests and wetlands as the dominating habitat type.

The one-variable models with ALAN and tree cover demonstrated higher predictive performance (AUC=0.62 and AUC=0.63) compared to the one-variable models with human density and NDVI (AUC=0.56 and AUC=0.59) and thus we selected ALAN and tree cover for further modelling. ALAN, cropland and tree cover were the strongest predictors of wolf presence (Fig. 2, Table 1). Land cover was also selected in the best-performing model (under alpha = 0.05), but main and tertiary road densities were not selected. Wolf presence was predicted to be high in places with very low ALAN values and the variable had the highest contribution to the model (Fig. 2b). A similar strong response was observed for cropland, showing a negative relationship with habitat suitability for wolves. Tree

cover was positively associated with the probability of wolf presence and the probability ratio output was > 1 if forested areas covered at least 1/5 of the grid cell (Fig. 2b). A probability ratio output of 1 represents the average suitability index across the study area, so all cells with > 20% tree cover are predicted to be more suitable than average (disregarding their values for other variables). Land cover
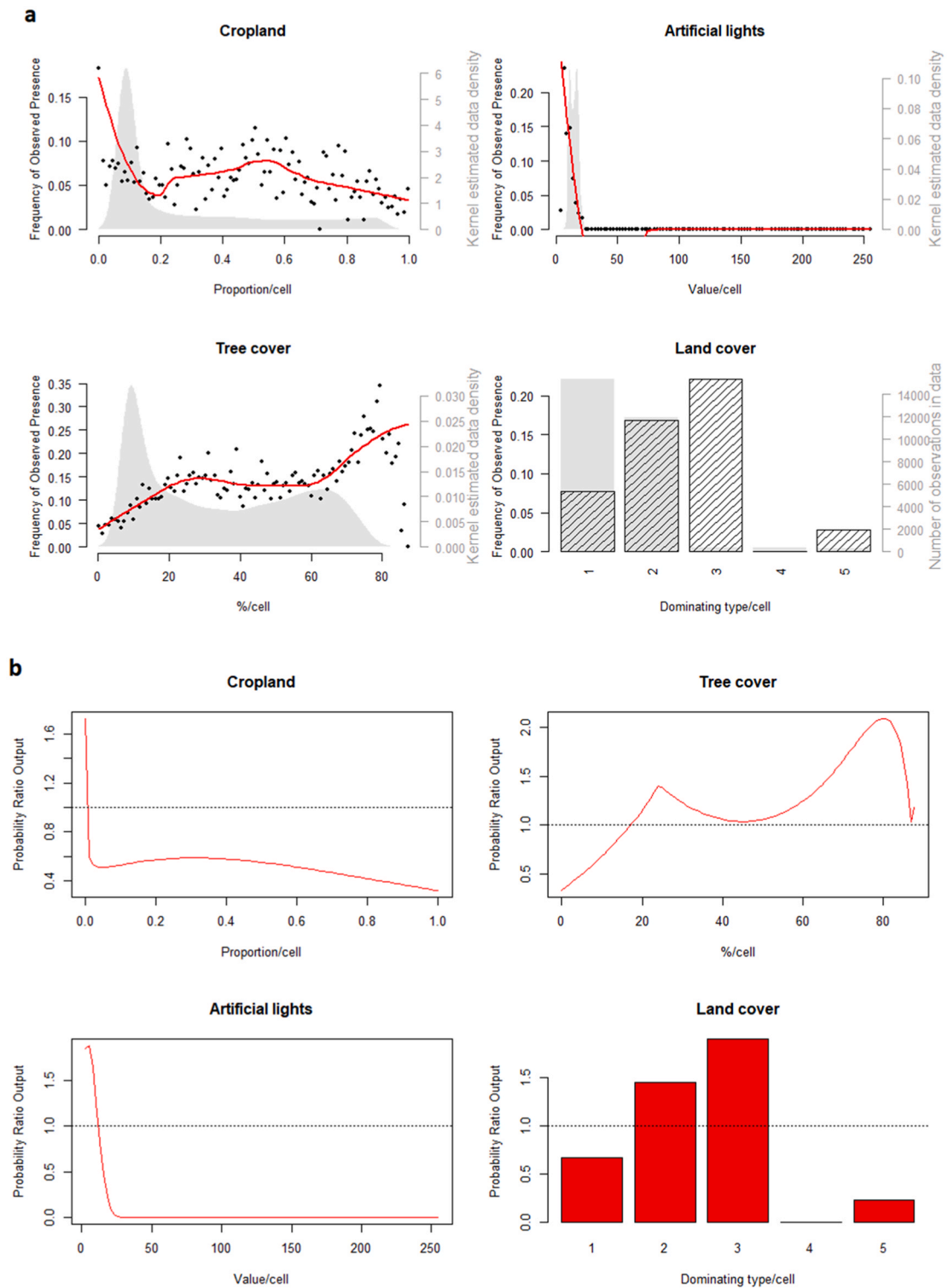

Fig. 2. The frequency of observed presence plots (top) and single-effect response curves (bottom) showing the changes in habitat suitability in the most important explanatory variables. Dominating land cover types: 1- open habitats; 2 – forests; 3 – wetlands; 4 – urban areas; 5 – water bodies.

types had a lower contribution to the model. The land cover types "forests "and "wetlands" had positive effects on the probability of wolf presence, while land cover types "open habitats", "urban areas" and "water bodies" had negative effects. The model's predictive performance on the spatially separate evaluation was good (AUC=0.80), and the AUC values decreased when dropping variables from
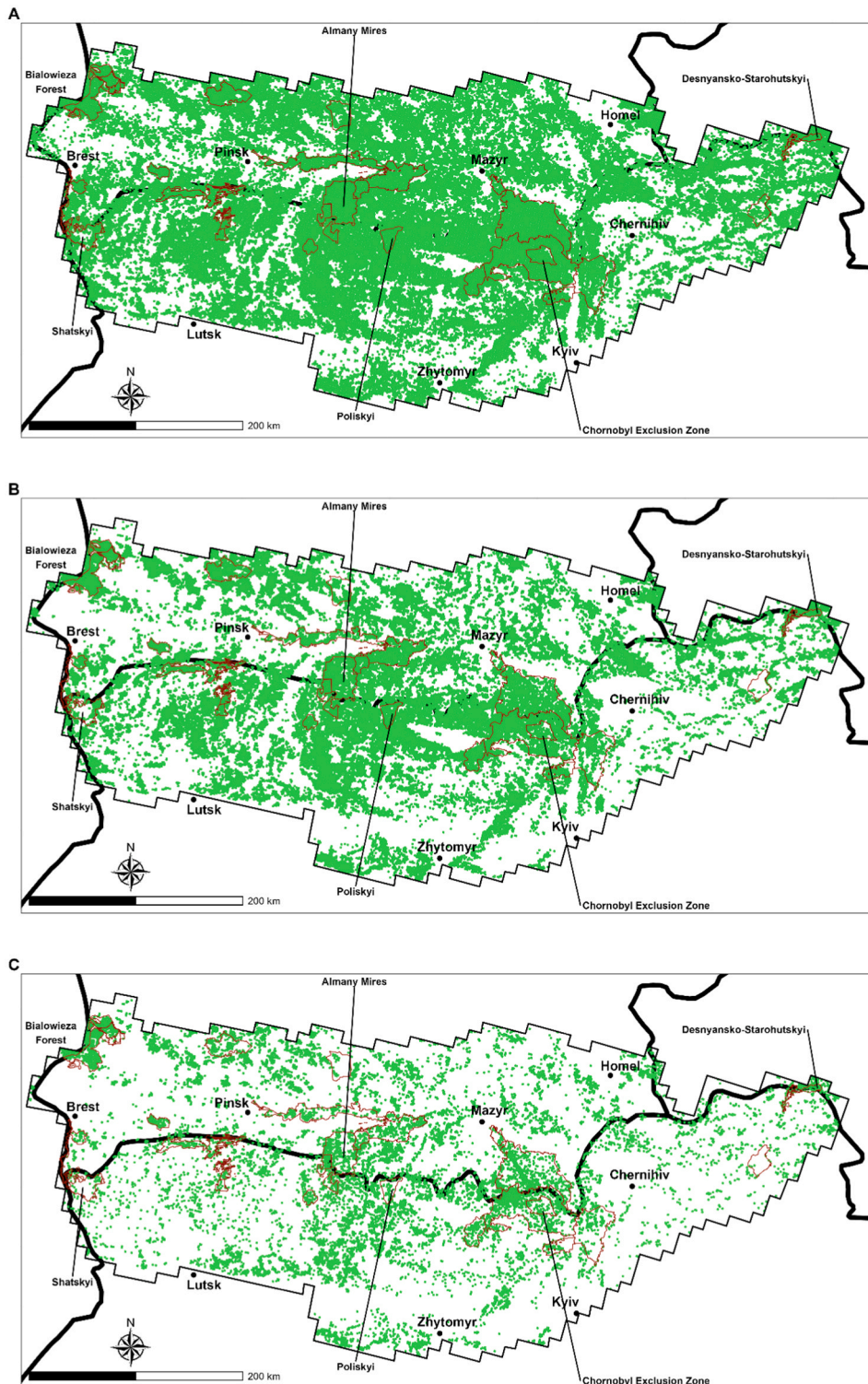

Fig. 3. Binary map of wolf in Polesia at 25th (**A**), 50th (**B**) and 75th (**C**) percentile thresholds. White = absence, green shade = presence. Masked areas indicate protected areas (>100 km²) across the region.

the selected model. Response curves followed the same patterns as the corresponding frequency of occurrence plots indicating that the best model captured empirical occurrence-environmental relationships (Fig. 2). We created habitat suitability maps by projecting the trained models onto the study area. Presence-only data allowed us to estimate relative probability of wolf presence within the study area. The best model graded 42,106 km^2 of Polesia (26%) as suitable (above the 50th percentile of presences), and 14,325 km^2 (9%) as highly suitable (above the 75th percentile of presences) (Fig. 3, Fig. B2). About 56% of Polesia (92,345 km^2) was estimated to have very low suitability values – lower than the 25% least suitable presence cells.

Our results revealed the core protected areas for wolf conservation – the Białowieża Forest, the CEZ with the neighboring Drevlyanskyi Nature Reserve and central Polesia (Almany Mires, Pripyatskyi and Mid-Pripyat National Parks and the Rivnenskyi Nature Reserve) were comprised of between 37% and 77% suitable habitat (50th percentile) within their territories (Fig. 3, Table A4). High-quality unprotected areas north of the Mizhrichynskyi Regional Landscape Park and Chernihiv city, between the segments of the Nobelskyi National Nature Park, Rivnenskyi and Poliskyi Nature Reserves and the CEZ, create a potentially permeable matrix between the core protected areas and thus are of conservation importance. The suitability maps demonstrated that national parks in western Polesia (Prypyat-Stokhid National Nature Park, Zvanets Nature Sanctuary) and in the easternmost part (Desnyansko-Starohutskyi National Nature Park) contain high-quality habitat patches isolated from the core protected areas (the Białowieża Forest, the CEZ) by surrounding low-quality habitat (Fig. 3, Table A4).

4. Discussion

Our results supported the growing body of studies showing the adverse effects of anthropogenic activities on habitat suitability for large carnivores. Our study highlighted how ALAN and cropland limit high-quality habitat available for the grey wolf in Polesia and identified hotspots of fragmentation in Polesia. In line with other European studies on large carnivores (Cimatti et al., 2021), our model has demonstrated that wolves avoid areas with permanent human presence and that highly suitable habitats are characterized by the absence of permanent human presence. Wolves also avoided areas where cropland was a dominating land cover type. Such preferences might be linked to vegetation alterations by farm animals that compete with wild herbivores (Flores-Morales et al., 2019) as well as to the duration and timing of human activities in agricultural fields. Wolves preferred areas with low levels of artificial light (max. 20). Satellite-based artificial light reflects human activities in high resolution (Mu et al., 2021) compared to widely applied human population density that fits for coarse-scale studies (Cimatti et al., 2021) yet may not capture regional and local differences in permanent human disturbance. ALAN is a reliable proxy for human disturbance in predicting habitat suitability particularly for places with less precise or outdated data on human footprint metrics. We proved that ALAN is a more reliable proxy for human disturbance than human density in our study area, as the former captures where people are and not where they should be according to census data.

The most suitable areas for wolves in Polesia are located in remote wetlands and forested areas. As in Poland (Jędrzejewski et al., 2008), our study revealed wolves' preference towards wetlands which are also a preferred habitat choice by wolf prey species (moose, wild boar and beaver) (Sidorovich et al., 2003). Wetland preference could be linked to forage quality (prey species) and avoidance of humans (prey species, wolf), as disturbance and hunting pressure might be higher near places with permanent human presence. Our habitat model identified suitable habitats for wolves within and outside PAs (Fig. 3, Table A4), even though two-thirds of wolf presences were collected in PAs. However, we could not directly evaluate whether protected areas are more suitable for wolves by adding protection status as an input variable because of the biased presence data. Highly suitable habitat patches were detected inside and outside the PAs without permanent resident wolf populations, particularly between the CEZ and central Polesia. Nonetheless, wolves may adapt to low-intensity human exposure since cells with low proportions of cropland were not predicted as completely unsuitable for the species. Moreover, wolves can travel long distances across low-quality habitats (Mech and Boitani, 2003; Gula et al., 2009; Byrne et al., 2018) to reach suitable areas yet the latter should be protected to become stepping stones securing the connectivity between potential source populations (the Białowieża Forest, the CEZ) and establishment of subpopulations in-between. Our model predicted suitable habitat (>50th percentile) within all regional protected areas large enough for at least one pack's home range that itself is highly fluctuating and can vary from 130 km^2 to over 390 km^2 (Shkvyria and Vishnevskiy, 2012; Smith et al., 2022). All suitable habitat patches in Polesia are reachable for wolves, but these patches should not be further fragmented. The accuracy of spatial extrapolation to the spatially separate evaluation dataset was satisfactory and encourages further modelling yet on the country level and by incorporating topographic and prey-related variables. Unlike in similar studies for mountainous regions (Kabir et al., 2017), we did not consider topographic variables (slope, altitude) and water availability due to landscape homogeneity and water abundance in Polesia (Marynych et al., 1985).

Road densities were not a deterring factor for wolves in Polesia as predicted for wolf populations in Finland and Poland (Kaartinen et al., 2005; Jędrzejewski et al., 2008) and were not selected in the most parsimonious model. Paved and unpaved secondary and tertiary roads with low disturbance prevail in the study area. Therefore, we suspect that wolves may not always avoid secondary and tertiary roads, but select roads with low traffic volume for moving within their home ranges (Zimmermann et al., 2014). However, collisions with vehicles were not reported to cause significant wolf mortality as in other places (Lovari et al., 2007), most likely because of low highway density and data deficiency.

Our results demonstrated that roughly one-quarter of Polesia is suitable for permanent wolf presence and breeding, but only a part of the predicted suitable area is permanently occupied. After the Chornobyl catastrophe (1986) followed by vanished or decreased human disturbance in a 30-km zone around the nuclear power plant, wolves have gradually re-colonized both the CEZ and the neighbouring Drevlyanskyi NR (Webster et al., 2016; Hinton et al., 2019). Official reports claim that wolves are present across Polesia, with population numbers estimated to be the highest among regional large carnivores (Niedziałkowski et al., 2022; Cherepanyn et al., 2023), yet long-term systematic research on large carnivores is still lacking in Belarus and Ukraine. Wolf occurrences are registered on

a regular basis only in several PAs while in other regional PAs and particularly outside them, wolf occurrences are rare (Table A4). Despite the refuge role of the CEZ (Deryabina et al., 2015), wolf distribution beyond its borders has barely changed since the 1980 s even after establishing smaller protected areas (e.g., Rivnenskyi Nature Reserve) most likely due to persisting wolf hunting, trapping and poisoning, especially outside the PAs (Shkvyrya et al., 2014). Wolves are still considered a vermin species and are hunted year-round both in Belarus and Ukraine. Human-related mortality in vast parts of Polesia may hamper effective colonization by dispersing individuals from the Białowieża Forest and the CEZ acting as sources. Therefore, evaluating how human-induced mortality affects species distribution in Polesia, Belarus and Ukraine is crucial. In accordance with conclusions in previous studies on large carnivores (Chapron et al., 2014; Bragina et al., 2015), we suspect that wolf culling as well as overhunting of wolf prey, may explain why wolves are not permanently present in areas that were predicted as suitable by our model. Inclusion of hunting-related data (wolf mortality, wolf prey mortality or licensed hunters' numbers) would complement future modelling.

Wolf distribution is determined by prey availability and human disturbance (Recio et al., 2018), and we had no data on prey availability or prey diversity for Polesia. NDVI has been included as a proxy of wild prey richness. However, NDVI encompasses habitat quality and cannot reflect the depletion of wild prey unless it is linked to vegetation loss. NDVI provides a good proxy for prey availability when the effect of hunting is minimal and well-documented. We suggest estimating wild prey abundance or diversity in Polesia in future studies. Regarding human disturbance, our model predicted higher suitability within regional PAs, which could have occurred because of two causes that we did not disentangle in this study: higher habitat suitability within PAs or higher sampling effort within PAs. Although we reduced the potential bias by considering wolf presence/absence per grid cell, we acknowledge that more presences outside the PAs or from less studied PAs might result in more accurate predictions of habitat suitability. However, PAs in Polesia mainly cover areas with natural vegetation and with low human disturbance where wolf core territories are more likely to occur. Consequently, establishing at least basic (species present/absent) systematic monitoring of wolves and their prey at least across all regional protected areas in Polesia is vital. For predicting habitat suitability in Belarus and Ukraine, we suggest developing habitat suitability models also at a coarse scale (first-order models) for delineating the wolf range at the country level (Stricker et al., 2019).

4.1. Conclusions

Conservation of wolves like other large carnivores requires preserving extensive core habitats, linkages between them, and mitigating human-wolf conflicts (Cushman et al., 2018). Habitat predictions revealed an extensive linkage zone between the CEZ and central Polesia which is important for efficient large carnivore conservation measures. Our results have also demonstrated that high-quality areas in the CEZ and nearby lack suitable habitat patches serving as stepping stones with the Desnyansko-Starohutskyi NP and Poliskyi NR (Ukraine). The Białowieża Forest was not well connected with PAs in the western part of Polesia, yet better linked with central Polesia. Our study results advocate for large interlinked PAs in central and eastern Polesia as they can sustain large carnivores by providing extensive refuges with a lower level of human disturbance and adequate prey abundance. Our model provides a foundation for expanding the existing network of protected areas (the Białowieża Forest, Mid-Prypyat NP in Belarus; Desnyansko-Starohutskyi, Prypyat-Stokhid, Nobelskyi NNPs, Rivnenskyi NR in Ukraine) and creating new protected areas in the vicinity of the Białowieża Forest and in the Belarusian part of eastern Polesia. Moreover, legal protection of wolves in Belarus and Ukraine may enhance the re-colonization of human-modified and less remote landscapes as reported in Europe (Chapron et al., 2014). Rural development and human activities in PAs are linked to landscape modification and changes in prey abundance that negatively affect large carnivores, especially when human encroachments are hardly regulated and their effects are not accurately studied.

Management actions that facilitate the preservation of extensive core habitat areas and connectivity between populations regardless of state borderlines can secure the viability of wolves and other large carnivores in the region. The coordinated efforts of state agencies at different levels in Belarus and Ukraine are crucial for efficient wolf conservation yet are becoming increasingly challenging. Due to extensive destruction of civil infrastructure and the environment in Ukraine since February 2022, including PAs, because of the full-scale Russian invasion from Belarus, adequate international cooperation and transboundary management for any wildlife species remain utopian. The occupation of some of Polesia's PAs in early 2022 disrupted the management of these areas and led to habitat degradation due to disturbance, pollution and changes in hunting pressure. Current military training, land mine placement, construction of a massive border wall and emplacements between Belarus and Ukraine (Lozovenko, 2022) will reduce the high-quality habitat, disrupt landscape permeability and fence off wolf populations in Belarus from the Baltic states' populations which have already been affected by a border fence that fragmented the Białowieża Forest and is now stretching along the Belarusian border with EU countries (Main, 2022). As civilian and armed conflict activities continue to increase in Polesia, wolf numbers can be expected to decline further, even in the wilderness areas.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

Disclaimer

This manuscript was prepared as an account of work sponsored by an agency of the United States Government. Neither the United States Government nor any agency thereof, nor any of their employees, makes any warranty, express or implied, or assumes any legal liability or responsibility for the accuracy, completeness, or usefulness of any information disclosed, or represents that its use not infringe privately owned rights. Reference herein to any specific commercial product, process, or service by trade name, trademark, manufacturer, or otherwise does not constitute or imply its endorsement, recommendation, or favouring by the United States Government or any agency thereof. The views and opinions of the authors expressed herein do not necessarily state or reflect those of the United States Government or any agency thereof.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02586.

References

Ballard, W.B., Carbyn, L.N., Smith, D.W., 2003. Wolf interactions with non-prey. In: Mech, L.D., Boitani, L. (Eds.), Wolves: Behavior, Ecology and Conservation. University of Chicago Press, Chicago.

Beresford, N.A., Copplestone, D., 2011. Effects of ionizing radiation on wildlife: what knowledge have we gained between the Chernobyl and Fukushima accidents? Integr. Environ. Assess. Manag 7 (3), 371–373. https://doi.org/10.1002/ieam.238.

Boitani, L., Linnell, J.D., 2015. Bringing large mammals back: large carnivores in Europe. In: Pereira, H.M., Navarro, L.M. (Eds.), Rewilding European Landscapes, pp. 67–84. https://doi.org/10.1007/978-3-319-12039-3_4.

Boitani, L., Phillips, M., Jhala, Y., 2018. *Canis lupus* (errata version published in 2020). IUCN Red. List Threat. Species 2018. https://doi.org/10.2305/IUCN.UK.2018-2.RLTS.T3746A163508960.en.

Bragina, E.V., et al., 2015. Rapid declines of large mammal populations after the collapse of the Soviet Union. Conserv. Biol. 29 (3), 844–853. https://doi.org/10.1111/cobi.12450.

Byrne, M.E., et al., 2018. Evidence of long-distance dispersal of a gray wolf from the Chernobyl Exclusion Zone. Eur. J. Wildl. Res 64 (4), 1–5. https://doi.org/10.1007/s10344-018-1201-2.

Chapron, G., et al., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346 (6216), 1517–1519. https://doi.org/10.1126/science.1257553.

Cherepanyn, R.M., et al., 2023. Population dynamics and spatial distribution of large carnivores in the Ukrainian Carpathians and Polissya. Biosyst. Divers. 31 (1), 10–19. https://doi.org/10.15421/012302.

Cieraad, E., et al., 2023. Artificial light at night affects plant–herbivore interactions. J. Appl. Ecol. 60 (3), 400–410. https://doi.org/10.1111/1365-2664.14336.

Cimatti, M., et al., 2021. Large carnivore expansion in Europe is associated with human population density and land cover changes. Divers Distrib., 2021 27, 602–617. https://doi.org/10.1111/ddi.13219.

Core Team, R., 2020. R: A language and environment for statistical computing. R version 4.0.1 (2020-06-06). R. Found. Stat. Comput., Vienna, Austria (Available at). ⟨https://www.R-project.org/⟩.

Cushman, S.A., et al., 2018. Prioritizing core areas, corridors and conflict hotspots for lion conservation in southern Africa. PloS One 13 (7), e0196213. https://doi.org/10.1371/journal.pone.0196213.

Deryabina, T.G., et al., 2015. Long-term census data reveal abundant wildlife populations at Chernobyl. Curr. Biol. 25 (19), R824–R826. https://doi.org/10.1016/j.cub.2015.08.017.

Didan, K., 2015. MOD13A3 MODIS/Terra vegetation Indices Monthly L3 Global 1km SIN Grid V006 [Data set]. NASA EOSDIS Land Process. DAAC. https://doi.org/10.5067/MODIS/MOD13A3.006. Accessed: 21.09.2022.

Dormann, C.F., et al., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36 (1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

Duffy, J.P., et al., 2015. Mammalian ranges are experiencing erosion of natural darkness. Sci. Rep. 5 (1), 1–6. https://doi.org/10.1038/srep12042.

Elith, J., et al., 2011. A statistical explanation of MaxEnt for ecologists. Divers Distrib. 17 (1), 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x.

Enserink, M., Vogel, G., 2006. The carnivore comeback. Science 314 (5800), 746–749. https://doi.org/10.1126/science.314.5800.746.

ESA, 2015, CCI-LC – Climate Change Initiative- Land Cover. Land Cover CCI. Product user guide Ver. 2. Available at: maps.elie.ucl.ac.be/CCI/viewer/download/ESACCI-LC-Ph2-PUGv2_2.0.pdf (Accessed 19.01.2020).

Estes, J.A., et al., 2011. Trophic downgrading of planet Earth. Science 333 (6040), 301–306. https://doi.org/10.1126/science.1205106.

Fiderer, C., Storch, I., Heurich, M., 2021, Schalenwildmonitoring in Deutschen Nationalparks AFZ/Der Wald. 1/2021. 12–16.

Flores-Morales, M., et al., 2019. Response of two sympatric carnivores to human disturbances of their habitat: the bobcat and coyote. Mamm. Res 64, 53–62. https://doi.org/10.1007/s13364-018-0385-x.

Gashchak, S., et al., 2017. European bison (Bison bonasus) in the Chornobyl Exclusion Zone (Ukraine) and prospects for its revival. Праці Теріол Школи. ⟨http://dspace.nbuv.gov.ua/handle/123456789/165935⟩.

Gaston, K.J., et al., 2021. Pervasiveness of biological impacts of artificial light at night. Integr. Comp. Biol. 61 (3), 1098–1110. https://doi.org/10.1093/icb/icab145.

Grilo, C., et al., 2019. Refuge as major habitat driver for wolf presence in human-modified landscapes. Anim. Conserv 22 (1), 59–71. https://doi.org/10.1111/acv.12435.

Guisan, A., Thuiller, W., Zimmermann, N.E., 2017. Habitat Suitability and Distribution Models: with Applications in R. Cambridge University Press,.

Gula, R., Hausknecht, R., Kuehn, R., 2009. Evidence of wolf dispersal in anthropogenic habitats of the Polish Carpathian Mountains. Biodivers. Conserv. 18, 2173–2184.

Halvorsen, R., Mazzoni, S., Bryn, A., Bakkestuen, V., 2015. Opportunities for improved distribution modelling practice via a strict maximum likelihood interpretation of MaxEnt. Ecography 38, 172–183. https://doi.org/10.1111/ecog.00565.

Hansen, M.C., et al., 2013. High-Resolution Global Maps of 21st-Century Forest Cover Change. Science 342, 850–853 (Data available on-line from). ⟨http://earthenginepartners.appspot.com/science-2013-global-forest⟩.

Hinton, T.G., et al., 2019. GPS-coupled contaminant monitors on free-ranging Chernobyl wolves challenge a fundamental assumption in exposure assessments. Environ. Int. 133, 105152 https://doi.org/10.1016/j.ecolmodel.2006.05.017.

Hirzel, A.H., et al., 2006. Evaluating the ability of habitat suitability models to predict species presences. Ecol. Model. 199 (2), 142–152.

Huck, M., Jędrzejewski, W., Borowik, T., Jędrzejewska, B., Nowak, S., Mysłajek, R.W., 2011. Analyses of least cost paths for determining effects of habitat types on landscape permeability: wolves in Poland. Acta Theriol. 56, 91–101.

Hundertmark, K., 2016, Alces alces. The IUCN Red List of Threatened Species 2016: e.T56003281A22157381. https://dx.doi.org/10.2305/IUCN.UK.2016–1.RLTS.T56003281A22157381.en. (Accessed 12.02.2022).

Jędrzejewski, W., et al., 2008. Habitat suitability model for Polish wolves based on long-term national census. Anim. Conserv 11 (5), 377–390. https://doi.org/10.1111/j.1469-1795.2008.00193.x.

Kaartinen, S., Kojola, I., Colpaert, A., 2005. . Finnish wolves avoid roads and settlements. Ann Zool Fennici. Finnish Zoological and Botanical Publishing Board,, pp. 523–532.

Kabir, M., et al., 2017. Habitat suitability and movement corridors of grey wolf (*Canis lupus*) in Northern Pakistan. PloS One 12 (11), e0187027. https://doi.org/10.1371/journal.pone.0187027.

Kehoe, L., et al., 2017. Biodiversity at risk under future cropland expansion and intensification. Nat. Ecol. Evol. 1 (8), 1129–1135. https://doi.org/10.1038/s41559-017-0234-3.

Longcore, T., Rich, C., 2004. Ecological light pollution. Front. Ecol. Environ. 2, 191–198. https://doi.org/10.1890/1540-9295(2004)002[0191:ELP]2.0.CO;2.

Lovari, S., et al., 2007. Mortality parameters of the wolf in Italy: does the wolf keep himself from the door? J. Zool. 272 (2), 117–124. https://doi.org/10.1111/j.1469-7998.2006.00260.x.

Lovari, S., et al., 2018. *Cervus elaphus* (errata version published in 2019). IUCN Red. List Threat. Species 2018. https://doi.org/10.2305/IUCN.UK.2018-2.RLTS.T55997042A142404453.en. Accessed 12.02.2022.

Lozovenko, T., 2022. Ukraine is building wall on border with Belarus. Ukr. Pravda. ⟨https://www.pravda.com.ua/eng/news/2022/11/11/7375956/⟩.

Main, D., 2022. Poland's border wall to cut through Europe's last old-growth forest. Natl. Geogr. Mag. ⟨https://www.nationalgeographic.com/environment/article/polish-belarusian-border-wall-environmental-disaster⟩.

Marynych, A.M., Pashchenko, V.M., Shyshchenko, P.G., 1985, Nature in Ukrainian SSR. Landcover types, physical and geographical mapping. Ed. Marynych, A.M. Kyiv. P. 29. (in Russian).

Maxwell, S.L., et al., 2016. Biodiversity: The ravages of guns, nets and bulldozers. Nature 536 (7615), 143–145. https://doi.org/10.1038/536143a.

Mech, L.D., Boitani, L., 2003. Wolf social ecology. In: Mech, L.D., Boitani, L. (Eds.), Wolves: Behavior, Ecology and Conservation. University of Chicago Press, Chicago, pp. 1–34.

Merow, C., Smith, M.J., Silander Jr, J.A., 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography 36 (10), 1058–1069. https://doi.org/10.1111/j.1600-0587.2013.07872.x.

Mindovkillya, 2021. Animal species added to and excluded from the national Red List. Minist. Environ. Prot. Nat. Resour. Ukr. (Mindovkillya). ⟨https://zakon.rada.gov.ua/laws/card/en/z0260-21?lang=uk⟩.

Mu, H., et al., 2021. Evaluation of Light Pollution in Global Protected Areas from 1992 to 2018. Remote Sens 13, 1849. https://doi.org/10.3390/rs13091849.

NASA Earth Observatory, 2017, Earth at Night, 500m resolution by region (C1, annual) (2016). Available at: ⟨https://earthobservatory.nasa.gov/features/NightLights⟩ (Accessed: 04.04.2022).

Niedziałkowski, K., et al., 2022. Stimuli and barriers to innovation in wildlife policy–long-term institutional analysis of wolf management in Belarus. Innovation. Eur. J. Soc. Sci. Res 35 (3), 460–480. https://doi.org/10.1080/13511610.2021.1995336.

Nowak, S., Mysłajek, R.W., Szewczyk, M., Tomczak, P., Borowik, T., Jędrzejewska, B., 2017. Sedentary but not dispersing wolves Canis lupus recolonizing western Poland (2001–2016) conform to the predictions of a habitat suitability model. Divers. Distrib. 23 (11), 1353–1364.

Potapov, P., et al., 2021. Global maps of cropland extent and change show accelerated cropland expansion in the twenty-first century. Nat. Food. https://doi.org/10.1038/s43016-021-00429-z (Data available at). ⟨https://glad.umd.edu/dataset/croplands/⟩.

QGIS.org, 2022. QGIS Geographic Information System. QGIS Assoc. (Available at) ⟨http://www.qgis.org⟩.

Recio, M.R., et al., 2018. Integrated spatially-explicit models predict pervasive risks to recolonizing wolves in Scandinavia from human-driven mortality. Biol. Conserv 226, 111–119. https://doi.org/10.1016/j.biocon.2018.07.025.

Redpath, S.M., et al., 2013. Understanding and managing conservation conflicts. Trends Ecol. Evol. 28 (2), 100–109. https://doi.org/10.1016/j.tree.2012.08.021.

Ripple, W.J., et al., 2014. Status and ecological effects of the world's largest carnivores. Science 343 (6167). https://doi.org/10.1126/science.1241484.

Ritchie, E.G., et al., 2012. Ecosystem restoration with teeth: what role for predators? Trends Ecol. Evol. 27 (5), 265–271. https://doi.org/10.1016/j.tree.2012.01.001.

Román, M.O., et al., 2018. NASA's Black Marble nighttime lights product suite. Remote Sens Environ. 210, 113–143. https://doi.org/10.1016/j.rse.2018.03.017.

Schipper, J., et al., 2008. The status of the world's land and marine mammals: diversity, threat, and knowledge. Science 322 (5899), 225–230. https://doi.org/10.1126/science.1165115.

Shkvyria, M., Vishnevskiy, D., 2012. Large carnivores of the Chernobyl Nuclear Power Pland Exclusion Zone. Vestn. Zool. 46, 21–28.

Shkvyrya, M., Parnikoza, I., Boreiko, V., 2014. Human-wolf co-existence in Ukraine (in Russian). Hist. Present 2, 127–134.

Sidorovich, V.E., 2011. Analysis of Vertebrate Predator-prey Community. Tesey,, Minsk, p. 736.

Sidorovich, V.E., Tikhomirova, L.L., Jędrzejewska, B., 2003. Wolf (*Canis lupus*) numbers, diet and damage to livestock in relation to hunting and ungulate abundance in northeastern Belarus during 1990–2000. Wildl. Biol. 9 (2), 103–111. https://doi.org/10.2981/wlb.2003.032.

Simpson, T.L., Thiel, R.P., Sailer, D.T., Reineke, D.M., Thomsen, M., 2023. Demographics of Gray Wolf (Canis lupus) Packs Recolonizing Variable Habitats in Central Wisconsin. Northeast. Nat. 30 (1), 75–98.

Smith, A.F., Ciuti, S., Shamovich, D., Fenchuk, V., Zimmermann, B., Heurich, M., 2022. Quiet islands in a world of fear: Wolves seek core zones of protected areas to escape human disturbance. Biol. Conserv 276, 109811.

SSC, 2020, Number and catching animals by species in 2020. State Statistics Service of Ukraine. Available from: ⟨https://ukrstat.gov.ua/⟩ (Accessed: 25.11.2022).

Stoner, D.C., et al., 2018. Climatically driven changes in primary production propagate through trophic levels. Glob. Chang Biol. 24 (10), 4453–4463. https://doi.org/10.1111/gcb.14364.

Stricker, H.K., et al., 2019. Multi-scale habitat selection model assessing potential gray wolf den habitat and dispersal corridors in Michgan, USA. Ecol. Model. 397, 84–94. https://doi.org/10.1016/j.ecolmodel.2018.12.021.

Trimaille, E., 2022, QuickOSM (OpenStreetMap) plugin version 2.0.1 for QGIS. Available at: ⟨https://docs.3liz.org/QuickOSM/⟩ (Accessed: 04.03.2022).

UkrBIN, 2017. UkrBIN: Ukrainian Biodiversity Information Network [public project & web application]. UkrBIN. Database Biodivers. Inf. ⟨https://www.ukrbin.com⟩.

UNEP-WCMC, IUCN, 2022. Protected Planet: The World Database on Protected Areas (WDPA) and World Database on Other Effective Area-based Conservation Measures (WD-OECM) [Online]. UNEP-WCMC and IUCN,, Cambridge, UK. ⟨www.protectedplanet.net⟩.

Vollering, J., et al., 2019. Bunching up the background betters bias in species distribution models. Ecography 42 (10), 1717–1727. https://doi.org/10.1111/ecog.04503.

Wabakken, P., et al., 2007. Multistage, long-range natal dispersal by a global positioning system-collared Scandinavian wolf. J. Wildl. Manag. 71 (5), 1631–1634. https://doi.org/10.2193/2006-222.

Webster, S.C., Byrne, M.E., Lance, S.L., Love, C.L., Hinton, T., Shamovich, D., Beasley, J.C., 2016. Where the wild things are: Influence of radiation on the distribution of mammalian species within the Chernobyl Exclusion Zone. Front. Ecol. Environ. 14 (4), 1–6.

Wenger, S.J., Olden, J.D., 2012. Assessing transferability of ecological models: An underappreciated aspect of statistical validation. Methods. Ecol. Evol. 3 (2), 260–267. https://doi.org/10.1111/j.2041-210X.2011.00170.x.

WorldPop, 2022a. Global High Resolution Population Denominators Project. Ukraine. School of Geography and Environmental Science, University of Southampton; Department of Geography and Geosciences, University of Louisville; Departement de Geographie, Universite de Namur) and Center for International Earth Science Information Network (CIESIN). Columbia University,. ⟨https://data.humdata.org/dataset/worldpop-population-density-for-ukraine⟩.

WorldPop, 2022b. Global High Resolution Population Denominators Project. Belarus. School of Geography and Environmental Science, University of Southampton; Department of Geography and Geosciences, University of Louisville; Departement de Geographie, Universite de Namur) and Center for International Earth Science Information Network (CIESIN). Columbia University,. ⟨https://data.humdata.org/dataset/worldpop-population-density-for-belarus⟩.

Zimmermann, B., et al., 2014. Behavioral responses of wolves to roads: scale-dependent ambivalence. Behav. Ecol. 25 (6), 1353–1364. https://doi.org/10.1093/beheco/aru134.