

Habitat models harnessing the power of heterogeneous occurrence data to inform species conservation in the context of rapid renewable energy expansion

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Abstract

In light of the ongoing transition of energy systems in Europe towards greater reliance on renewable resources, climate protection and biodiversity conservation need to be harmonised. Germany is fast-tracking the construction of renewable energy in accordance with the EU Renewable Energy Directive (RED III) and national legislation. To mitigate potential conflicts with nature conservation, the 2022 revision of the German Federal Nature Conservation Act incorporated national recovery programmes for the species at risk. However, comprehensive biodiversity data that could inform the prioritisation of nature conservation interests in the field, is widely lacking in responsible authorities. To represent the habitat requirements and nationwide breeding distributions of eleven large-bodied bird species threatened by wind turbine collisions, we set up a modelling framework to unify the available heterogeneous occurrence data from governmental and non-governmental sources. By using hierarchical spatial distribution models, we derive species specific predictions of habitat suitability and probability of occurrence in Germany. The results show good quality in validation and are consistent with the known broad-scale distributions of the individual species as well as their combinations, as observed in Atlas surveys conducted in Germany. The model results therefore provide the most up-to-date, detailed and comparable information on the nationwide breeding distributions and habitat preferences of the considered species. We provide public access to our methods and the results and will integrate future work into a version history (currently v. 1.0). When applying the model results in practice, it is essential to consider existing limitations and inherent uncertainty. We discuss important aspects for users to consider. Despite limitations, the approach successfully captures the best information currently available and expands the possibilities in situations with limited data availability.

Keywords: habitat suitability, occurrence probability, sdmTMB, hierarchical spatial distribution models, wind power plants

Introduction

To reduce greenhouse gas emissions under the Green Deal strategy, the energy sector in the European Union is undergoing a profound transformation towards renewable energy sources (Widuto, 2023). With the revision of the Renewable Energy Directive in 2023 (RED III), an EU average target of 42.5 % renewable energy was established for 2030 EU Directive 2023/2413, with national states setting their own contributions to the target (Widuto, 2023). Germany is currently one of the leading countries in Europe with more than 66 GW wind energy capacity installed (Wolniak and Skotnicka-Zasadzień, 2023). In 2022 the German Federal Government set a binding target to approve an area of 2 % of the country for wind turbine construction until 2032 and aimed

for an increase of the wind energy capacity in Germany to 157 GW until 2035 (Bundesgesetzblatt, 2022).

Despite the benefits of renewable energy for climate protection, construction and operation of renewable energy infrastructures can also threaten biodiversity and increasing renewable energy production potentially exacerbates conflict with nature conservation interests. Especially wind energy turbines are well known to cause detrimental collision mortality for some long-lived bird and bat species (Bellebaum et al., 2013; Heuck et al., 2020; Hurst et al., 2016; Länderarbeitsgemeinschaft der Vogelschutzwarten, 2014; Voigt et al., 2022) as well as large-scale disturbance and habitat loss for these taxa (Peschko et al., 2024; Reusch et al., 2022; Thaker et al., 2018). Reconciling the operation of wind turbines with nature conservation is best achieved with thorough environmental impact assessments (EIA) and careful site-selection, however, this process is time consuming and falters under rapidly expanding production targets and increasing energy requirements. Clearly, biodiversity worldwide is under extreme pressure (IPBES, Díaz et al. 2019). and the conservation of healthy plant and animal populations is of critical importance (CBD, 2022), thus the accruing rapid expansion of renewable energies needs to be harmonised with biodiversity protection and species conservation.

To facilitate the large-scale energy transition, legislation on EU and national level in the RED III directive was put forward to prioritise and fast-track renewable energy construction over other locally conflicting interests, by implementing the mandatory designation of so called “Renewable Acceleration Areas” (RAA), where EIAs and local surveys of threatened species are no longer necessary. To address some of the foreseeable negative impacts on biodiversity of prioritising renewable energy production, the German Federal Government in 2022 revised the Federal Nature Conservation Act by listing 15 large-bodied breeding bird species as threatened by wind turbine collisions and instituting national species recovery programmes aiming to upscale protection measures for the species under threat (§ 45b & d Bundesnaturschutzgesetz (2022a)). Yet, in practice, it is often unclear which sites are especially vulnerable to energy infrastructure development and where habitat conditions are most favourable for the species at risk, because up-to-date, comprehensive and comparable biodiversity occurrence data is lacking in the responsible regional, federal and national authorities. Thus, it is also largely unclear, where best to direct the limited available funding for effective species conservation and how to mitigate future conflict between on-the-ground conservation measures and ongoing energy infrastructure development.

To address the need for better data to inform large- and small-scale planning of species protection measures for wind turbine collision-sensitive breeding bird species, we designed a project harnessing the strengths of the currently available heterogeneous occurrence data from governmental and non-governmental sources and hierarchical species distribution models with explicit spatial components.

Methods

Data basis and data preparation

We gathered data on breeding bird occurrences for the 15 bird species listed as sensitive to wind turbine collision in the German Federal Nature Conservation Act. To gather data on breeding sites and territories of these species across their distribution range in Germany, we included data from data bases of the federal states and from the national data base *ornitho.de* in our analysis. These

data sources mostly include unstructured data not originating from targeted surveys of these species but are curated by regional experts. Data from structured surveys are only available for single species, years and federal states.

Data bases of the federal states

A data request on breeding sites and territories for the years 2010-2023 was submitted to the responsible authorities of the federal states in Germany. The data feedback varied depending on the bird species and federal state (see supplementary material, Tab. S1). Data was submitted to us from all federal states except Mecklenburg-Western Pomerania and for two rare bird species (Golden Eagle and Lesser Spotted Eagle). Due to their locally restricted breeding distribution and low data availability, we subsequently excluded these two species as well as Short-eared Owl and Hen Harrier from further analysis. Data collection and modelling for Montagu's Harrier was conducted in a separate project, data basis and preparation are detailed in Vansynghel et al. (unpublished) and Dellwisch & Katzenberger (in prep).

To allow for a uniform manipulation of the federal states' data, we created a standardised format including information on species, year, coordinates (EPSG:25832) and Atlas Codes giving information on behaviour assigned to the observations. Atlas Codes categorize species observations by behaviour into broad classes of A: possible breeding, B: likely breeding and C: confirmed breeding and more detailed information on breeding time behaviour can be given (for more details, see: https://www.ornitho.de/index.php?m_id=41&lang=en). We only included observations with likely or confirmed breeding behaviour detected - Atlas Codes B and C - in our analysis. We also tested for possible duplicate observations per year and species within 5 m distance, i.e. in a 2.5 m radius around each observation. If potential duplicates were detected, the data point with the highest Atlas Code was retained, otherwise a random point was chosen.

National data base ornitho.de

We subsequently added data from *ornitho.de* to the data set provided by the federal states. The citizen science platform *ornitho.de* contains over 80 million high-quality casual observations of birds in Germany, with over 10 million new records added annually by tens of thousands of volunteers and validated by hundreds of regional coordinators. *Ornitho.de* is operated by DDA e.V. and its regional member organisations. Since the inception of the observation platform in 2011, the data collection for the voluntary national bird monitoring schemes has been subsequently integrated within *ornitho.de* as well (<https://www.dda-web.de/ornitho/info>). We excluded data entries marked as questionable by regional coordinators as well as records with zero abundance and "A" Atlas Codes. We restricted data to the breeding time of the species according to the months containing 95 % of the breeding observations with B and C Atlas Codes (Tab. 1). As comments in the data suggested wrong classification of Atlas Codes for Osprey in the early period of March, we further restricted data for this species to observations after 10th of March of each year.

Combination of data sources

To avoid adding data referring to the same breeding sites already present in the federal states' data, observations from *ornitho.de* were only added outside a 1 km buffer around existing data points and by applying additional data filters. Outside this buffer area, data from *ornitho.de* were added in a stepwise procedure according to their data quality (Atlas Code and accuracy).

Observations with exact coordinates of confirmed breeding sites (Atlas Code C) were buffered by a species-specific radius (Tab. 1). Observations of possible breeding sites were then only added if located outside this species-specific buffer and thus possibly indicating an additional territory or breeding site. The remaining data points were then used as a basis to add spatially less accurate data that have been entered to ornitho.de based on an underlying grid with cell size of approximately 1 km². These data were added only if they laid in distance of more than 1 km to the already filtered exactly located data points. The least accurate data in ornitho.de, those entered for so-called “sites”, such as the centre of parks or nature reserves, were only added if located in at least 1 km distance to all already filtered data points. At last, we checked for duplicate entries per territory using the species-specific buffer values derived from information on home ranges, distances between breeding sites or similar information potentially describing the area around breeding sites used by a species based on Mebs & Schmidt (2006) and additional data sources (Tab. 1). Within these assumed territories around potential or certain breeding sites, we kept only one data point with the most reliable information following a stepwise filter approach primarily using the highest Atlas Code and subsequently the maximum of the number of columns with available information on the observations, the minimum observer ID, the maximum of month and the minimum of day. If all values were equal, a sample point per territory or breeding site was chosen randomly.

Table 1: Overview of selected species and the breeding season range for which available data were considered. Months were selected based on the 2.5 % and 97.5 % quantiles for which data with B and C Atlas Codes were available on ornitho.de. A species-specific buffer radius based on Mebs & Schmidt (2006) and the listed references was used around observations with confirmed breeding to preclude duplicate data on potential breeding sites being added.

Species	Scientific name	month q2.5	month q97.5	Buffer radius (m)	Reference
Eurasian Eagle-Owl	<i>Bubo bubo</i>	1	7	500	Miosga et al. 2019
White Stork	<i>Ciconia ciconia</i>	3	7	1500	
Western Marsh Harrier	<i>Circus aeruginosus</i>	4	7	500	Cardador et al. 2009
Montagu’s Harrier	<i>Circus pygargus</i>	5	8	750	Dellwisch & Katzenberger (in prep)
Peregrine Falcon	<i>Falco peregrinus</i>	1	7	1500	
Eurasian Hobby	<i>Falco subbuteo</i>	4	8	1500	Sergio et al. 2001
White-tailed Eagle	<i>Haliaeetus albicilla</i>	1	8	2500	Heuck et al. 2019
Black Kite	<i>Milvus migrans</i>	3	7	1500	
Red Kite	<i>Milvus milvus</i>	3	7	1000	Hötker et al. 2017, Pfeifer & Meyburg 2015
Osprey	<i>Pandion haliaetus</i>	3	7	2000	Meyburg et al. 2023
European Honey-buzzard	<i>Pernis apivorus</i>	5	8	2500	Gamauf et al. 2013

Spatio-temporal filter of available data

To consider differences in spatial and temporal data availability, we compared the number of available data points per species for the period 2018-2023 within approx. 10x10 km raster cells of

the TK25 topographic map to known abundance class for the respective cell according to the most recent German Breeding Bird Atlas survey (2005-2009) from Gedeon et al. (2014). We then used only occurrence data from 2018-2023, if the number of data points was higher than the geometric mean of the abundance class from Atlas surveys of the raster cell. To obtain a balanced picture of the distribution of the species, we additionally used data from 2010 onwards if the number of observations within a quadrant was lower than the geometric mean of the respective abundance class. If again this value was not reached for a certain cell, all available observations from 2000 onwards were used. However, most of the data (59 % - 92 % per species) was available for the period 2018-2023, reaching levels of 96 % - 100 % per species when adding data back to 2010. Only very few observations dating back to 2000 were included (Tab. S2). We also distinguished between the number of available C and B observations and between categories of data quality (high: federal states' and precise ornitho.de data, low: quadrant and site-based information from ornitho.de). Data of high quality alone and C Atlas Codes were used in regions with high data availability, while in regions with low data availability, less accurate data as well as B Atlas Codes were added.

Creation of pseudo-absences

Pseudo-absences were drawn as random points within a distance of 20 km around the presence points, so that absence points are most likely not drawn outside the species' distribution range. Random points within one kilometre of the presence locations were excluded to rule out a strong overlap of the pseudo-absences with sites frequently used by the species. The number of pseudo-absences was equal to the number of data points before applying the spatio-temporal filter. As the data basis varied between the federal states, the number of presence points per federal state was set in relation to the total number of presence points across Germany and this ratio per state was used as a weighting factor to draw a sample of pseudo-absences also reflecting the regionally differing data availability. In addition, the ratio of how many presence points were located within and how many were located outside the last known distribution range of the respective species (Bundesamt für Naturschutz, 2019; Gerlach et al., 2019) was used as a second weighting factor while drawing the final sample of pseudo-absences with an equal number of points as the presence data per species (Fig. S1).

Preparation of environmental variables

Environmental variables on land cover, land use, topography and climate were considered to characterise the landscape around the focal presence/pseudo-absence points (Tab. 2). Data with a resolution of 5000 m edge length was disaggregated to 1000 m edge length and polygonal data was rasterized using package terra to resolutions of 100 m and 1000 m edge length (Hijmans et al., 2024) in R v. 4.4.0 (R Core Team, 2024). All data were harmonised to a common coordinate reference system (CRS), namely EPSG:25832 (ETRS89 / UTM zone 32N). Depending on the spatial resolution of the available environmental variables, larger or smaller areas around the focal points were used to characterise the surrounding landscape. For all raster data with a resolution greater than 1000 m edge length, a buffer area of 2000 m around the points was used; for raster data with a lower resolution, a 500 m radius around the points was used.

Information on monthly average temperatures, precipitation sum, and sunshine duration were gathered from the DWD Climate Data Centre for the years 2018 until 2022. Averages were calculated across all breeding time months and species according to Tab. 1 and for the non-

Table 2: Environmental parameters considered and processed for modelling the probability of occurrence and habitat suitability of wind turbine collision-sensitive breeding bird species.

Variable	available spatial resolution	available temporal resolution	years	unit	source
Average temperature	raster, 1000m	monthly values	2018-2022	5yrs-mean [$^{\circ}\text{C} \times 10$]	DWD ¹
Average sunshine duration	raster, 1000m	monthly values	2018-2022	5yrs-mean [sum in h]	DWD ¹
Average precipitation	raster, 1000m	monthly values	2018-2022	5yrs-mean [sum in mm]	DWD ¹
Corine Land Use Categories	raster, 100m	one year	2018	classes of land cover (in total, 36 classes used for Germany) proportion of overlap with raster cells	BKG ²
Settlements	raster, 100m	one year	2018	covering settlements [%]	BKG ²
Wetlands	raster, 100m	one year	2018	proportion of overlap with raster cells covering larger lakes and rivers [%]	BKG ²
Open land	raster, 100m	one year	2018	proportion of overlap with raster cells covering arable and grasslands [%]	BKG ²
Organic farming	raster, 5000m	one year	2020	ratio of organic to agric. land [%], categorical values transformed to numerical scale (see Tab. S3)	Agraratlas ³
Large livestock units	raster, 5000m	one year	2020	large livestock units per 100 ha agric. land, categorical values transformed to numerical scale (see Tab. S3)	Agraratlas ³
Grassland	raster, 100m	one year	2020	ratio of grassland to admin. area/territorial unit [%]	IÖR-Monitor ⁴
Road network	raster, 100m	one year	2020	length of the non-classified road network per admin. area/territorial unit [km/km ²]	IÖR-Monitor ⁴
Street network	raster, 100m	one year	2020	length of the classified road network per admin. area/territorial unit [km/km ²]	IÖR-Monitor ⁴
Relief variety	raster, 100m	one year	2012	ratio of real surface area to planimetric area of admin. area/territorial unit	IÖR-Monitor ⁴
Woody edge structures	raster, 100m	one year	2020	edge length of forests, groves, hedges, tree rows per admin. area/territorial unit [km/km ²]	IÖR-Monitor ⁴
Soil quality rating	raster, 250m	-	-	value for soil quality of agricultural land within a possible range from 0 and 102 points [-]	(Müller et al., 2007)
Tree species diversity	raster, 10m	combined years	2017-2018	dominant tree species within rastercell	(Blickensdörfer et al., 2022)
Proportion of deciduous trees	raster, 10m	combined years	2017-2018	dominant tree species within rastercell used to calculate proportion around point data	(Blickensdörfer et al., 2022)
Proportion of coniferous trees	raster, 10m	combined years	2017-2018	dominant tree species within rastercell used to calculate proportion around point data	(Blickensdörfer et al., 2022)
Median day of first mowing event	raster, 10m	one year	2017-2022	date of first mowing event used to calculate median around point data	(Schwieder et al., 2021)
Crop diversity	100ha hexagons	yearly values	2017-2022	diversity metric "Simpson's diversity index" of the agricultural field crops [-]	(Tetteh et al., 2023)
Relative crop edge density	100ha hexagons	yearly values	2017-2022	Relative edge density in the agricultural landscape compared to average in 50km around a focal cell [m/ha = m/m ² *10000]	(Tetteh et al., 2023)

¹ DWD: https://opendata.dwd.de/climate_environment/CDC/grids_germany/monthly/

² BKG: GeoBasis-DE / BKG (2023)

³ Agraratlas: <https://agraratlas.statistikportal.de>

⁴ IÖR-Monitor: Leibnitz-Institut für ökologische Raumentwicklung (2023)

breeding season from November until February. CORINE raster data on land cover was gathered from GeoBasis-DE / BKG (2023) and the proportion of raster cells of categories of settlements, wetlands and open land (arable and grassland) were calculated. Information on tree species (10 m) from Blickensdörfer et al. (2022) was used to calculate the shannon-diversity of tree species with package *vegan* (Oksanen et al., 2020). In addition, the proportion of deciduous trees and coniferous trees for wooded raster cells was derived while cells where no tree species were detected were set to 0. Information on edge density on agricultural land for Germany from Tetteh et al. (2023) was used as information on available field edges. As there is a strong difference in field size between eastern and western Germany (Frank et al., 2024), we derived the relative edge density of a raster cell (100 m) compared to an average edge density in a 50 km focal window around that cell using a moving window approach to be able to compare regional differences rather than confounding broad-scale patterns in configuration of agricultural landscapes.

For spatial projections of the model results, a raster layer with 1000 m edge length was created across Germany for each of the variables used. Unless otherwise described, the arithmetic mean of the raster cell values was calculated.

Statistical modelling

Species distribution models were calculated for each species using the *sdmTMB* package with default priors (Anderson et al., 2024), allowing efficient calculation of hierarchical distribution models with spatial components similar to the INLA approach (Anderson et al., 2024; Rue et al., 2009). The models we used separately consider the effects of the environmental variables on the occurrence of the species (further termed habitat suitability) as well as additional spatial dependencies in the data not explained by the considered environmental variables using so-called Gaussian Random Fields (GRF). Together, these separate model parts reflect the probability of occurrence of the respective species (Anderson et al., 2024). The GRF was created based on a species-specific mesh using a k-means algorithm based on a given number of knots per species (Tab. 3). The number of knots was broadly set relative to data availability (Tab. 3) with a minimum number of 300 knots (Latimer et al., 2009). The number of knots was however reduced for Peregrine Falcon and European Honey-buzzard due to convergence issues.

We split species datasets into training and testing data by 80 % to 20 % and used the training data to delineate the environmental factors with strongest impacts on species' occurrence probability. As the requirements of the species differ, we did not consider all environmental variables for each species model, but only those variables that could conceivably influence their occurrence based on their ecology. To this end, we categorised the species into the following groups: species using primarily farmland to forage and or to breed, species that also feed on large insects, species associated with wetlands and those that are bound to relief- and settlement breeding sites. The variables used (Tab. 4A) and the interactions between the main effects differ according to species group affiliation (Tab. 4A, Text S1). Where possible a quadratic effect was also included in the first model run. Exceptions with linear effects only were organic farming and large livestock units due to the original ranks of the data (Tab. S3) and the proportion of coniferous trees, crop diversity and relative crop edge density due to convergence issues, the latter was only true for farmland bird species. All variables were standardised and centred to their mean. We then assessed variance inflation factors for all main effects using package "performance" (Lüdecke et al., 2021) on a binomial model in package *glmmTMB* (Brooks et al., 2017).

Table 3: Number of knots used to create a species-specific mesh with a k-means algorithm.

Species	Number of vertices (n_knots)	N (presence points)
Eurasian Eagle-Owl	300	4880
White Stork	500	18786
Western Marsh Harrier	500	11495
Montagu's Harrier	400	2015
Peregrine Falcon	200	3900
Eurasian Hobby	300	4197
White-tailed Eagle	300	2665
Black Kite	400	8982
Red Kite	600	27603
Osprey	300	2222
European Honey-buzzard	250	2918

The set of variables used for the initial model run was then reduced to the most relevant environmental variables for each species by a backward model selection approach using the 95 % confidence interval of the effect sizes (Tab. 4B). First, quadratic effects or interactions with lowest Z-values (<1.96) were excluded from the model and refitted. Once all variables showed Z-values >1.96 , model selection was stopped. This was repeated for main effects only but excluding those main effects for which interactions of quadratic effects or interactions already showed Z-values >1.96 from further model selection. We further assessed goodness of model fit on the testing data using AUC (Area Under Curve) from package pROC (Robin et al., 2011) and Pseudo- R^2 using package ModEVA (Márcia Barbosa et al., 2013) for both model predictions based on effects of the environmental variables only (habitat suitability) and environmental effects plus GRF (occurrence probability). The finally selected model was checked for convergence issues using function “sanity” in sdmTMB (Anderson et al. 2024) and then used to derive predictions across Germany based on a 1 km grid. We detected high values in gradient length for European Honey-Buzzard, Peregrine Falcon and Black Kite and therefore refitted models with function ‘run_extra_optimization’ applying extra optimization loops to aid convergence. We further visually assessed normality of model residuals and patterns in spatial autocorrelation.

To characterise habitat suitability of the species we derived predictions based on the effects of environmental variables alone. To describe the probability of occurrence of each species, we used values of habitat suitability and incorporated the deviation from these predictions based on the GRF. To evaluate patterns in occurrence and habitat suitability throughout Germany across all species, we calculated the arithmetic mean and median per raster cell and the standard error to describe deviation from the mean (Fig. 1A, C & D). To make species-specific values comparable across species, we standardised all values from 0 to 1 beforehand. We also aggregated the most recent available information on species distribution based on information on their occurrences from Gedeon et al (2014) counting the number of species present in the survey from 2005-2009 per TK25 grid cell (Fig. 1B).

Table 4: Overview of A) variables considered for the models depending on the species' affiliation to one of the species groups (highlighted in colour). For full initial model formulas see Text S1. In B) effect sizes of linear main terms selected in the final model are shown for each species. A negative quadratic effect is indicated by ^{-q}, a positive quadratic effect by ^{+q}. Statistically significant main effect sizes or quadratic effects are shown in bold. For more information on coefficients of parameters and their interactions see Tab. S4. *data preparation and modelling for Montagu's Harrier was done in a separate project (see Methods section), therefore variables used partly differed: weather-data for the non-breeding period were averaged from January to April, open land area was aggregated using the sum of grassland and arable land from Leibnitz-Institut für ökologische Raumentwicklung (2023) instead of derived quantities from Corine Land Cover from GeoBasis-DE / BKG (2023). Additionally, the area of protected sites (nature reserves, NATURA2000 sites and national parks from IÖR-Monitor 2023) was used and selected (0.50) as variable for Montagu's Harrier.

A) Variables used per species group					B) Variables selected during variable selection											
Variable	farmland	wetlands	insectivorous	building/relief	Montagu's Harrier*	Red Kite	Black Kite	Marsh Harrier	White Stork	White-tailed Eagle	Osprey	Eurasian Hobby	European Honey-Buzzard	Eagle - Owl	Peregrine Falcon	Montagu's Harrier*
Avg. temperature breeding	x	x	x	x	x	0.16	1.29 ^q	0.88	1.07	0.66 ^q	0.73	0.44		0.23	0.19	-2.15 ^q
Avg. sunshine duration breeding			x		x*											
Avg. precipitation breeding	x	x	x	x	x	0.12	-0.17	-0.88 ^q	-1.12 ^q	-0.81				-0.26 ^q	-0.65	
Avg. temperature non-breeding			x		x*							0.21 ^q	0.21			
Avg. sunshine duration non-breeding			x		x											
Avg. precipitation non-breeding			x		x*							-0.28 ^q				-2.48
Corine Land Use Categories					x											x
Settlements	x	x	x	x		-0.28 ^q	-0.24 ^q	-0.04 ^q	0.36 ^q	-0.21	-0.18	-0.14	-0.30	0.26	0.64	
Wetlands	x	x	x			0.17 ^q	1.14 ^q	1.68 ^q	0.36 ^q	1.28 ^q	1.18 ^q	0.55 ^q	0.04			
Open land	x	x	x	x	x*	-0.08 ^q	-0.11 ^q	0.09 ^q	0.01 ^q	-0.92	0.53 ^q	-0.03 ^q	-0.73 ^q	-0.33 ^q	-0.19	2.02
Organic farming	x		x		x	0.07	-0.11 ^q		0.04					-0.08		0.03
Large livestock units	x		x		x		0.09	-0.13	0.02			-0.12	-0.11			-0.25
Grassland	x	x	x	x		0.42 ^q	0.67 ^q	0.21	1.51 ^q	0.12 ^q	0.18	0.31	0.07	-0.42 ^q	-0.25 ^q	
Road network	x	x	x	x	x	-0.11 ^q	0.17 ^q	-0.10	0.21 ^q	-0.42 ^q	-0.28 ^q	-0.25	-0.14	0.00 ^q		-0.18
Street network	x	x	x	x	x	-0.22 ^q	-0.70	-0.49 ^q	1.92 ^q	-1.27 ^q	-0.53	-0.83	-0.74 ^q	-0.56 ^q		
Relief diversity	x	x	x	x	x	-0.12 ^q	-0.65	-0.83	-1.47		0.27	-0.65		2.29 ^q	1.76 ^q	-4.38 ^q
Woody edge structures	x	x	x	x	x	0.43 ^q	0.52 ^q	0.03 ^q	-0.01	0.56	0.78	0.22	0.32 ^q	0.69 ^q	0.39 ^q	-1.51 ^q
Soil quality rating	x		x	x	x		0.14	-0.24 ^q	0.19			-0.11 ^q	-0.18 ^q	0.22 ^q		0.37
Tree species diversity	x	x	x	x		0.07 ^q	0.08	0.10	-0.06	-0.30 ^q	0.33 ^q	0.11	0.15	0.13	-0.12	
Proportion of deciduous trees	x	x	x	x		0.43	0.35	-0.05				0.03	0.19		-0.10	
Proportion of coniferous trees	x	x	x	x		0.13	-0.10	-0.48	-0.37	-0.23			0.43	-0.15	-0.24	
Median day of first mowing event	x	x	x	x		0.12 ^q	-0.02 ^q	0.53 ^q	-0.11 ^q	0.19 ^q		0.15 ^q	0.12			
Crop diversity	x	x	x	x	x	0.03	0.04	0.17	0.12					0.16	-0.21	
Relative crop edge density	x		x				-0.18		-0.51							

Results

We provide version 1.0 of our results as figures, tables and data layers with this work (see supplementary materials). All models converged and achieved acceptable (>0.7) to very good (>0.9) AUC values for both predictions of occurrence probability and habitat suitability (Tab. 4). The proportion of variance explained by the models ranged from 20 to 84 %. By accounting for spatial dependencies in the data, the classification ability of the models and the explained variability increased substantially (Tab. 4). Variance Inflation Factors showed low collinearity ($VIF < 5$) (James et al. 2013) for all variables included and very low values ($VIF < 3$) in most cases (Zuur et al. 2010). The resulting model predictions depict habitat suitability and occurrence probability for the respective species across Germany at a scale of 1 x 1 km (Fig. 2).

Table 4: Criteria of goodness of fit for species models differentiated between habitat suitability (effects of environmental variables only) and occurrence probability (including Gaussian Random Fields).

Species	Occurrence Probability		Habitat Suitability	
	AUC	R ²	AUC	R ²
Eurasian Eagle-Owl	0.85	0.46	0.77	0.29
White Stork	0.93	0.71	0.90	0.59
Western Marsh Harrier	0.86	0.50	0.76	0.29
Montagu's Harrier	0.98	0.84	0.92	0.67
Peregrine Falcon	0.83	0.40	0.80	0.35
Eurasian Hobby	0.82	0.38	0.75	0.24
White-tailed Eagle	0.84	0.42	0.73	0.20
Black Kite	0.86	0.49	0.79	0.32
Red Kite	0.83	0.40	0.72	0.20
Osprey	0.83	0.42	0.73	0.23
European Honey-Buzzard	0.78	0.32	0.74	0.24

Important environmental effects

Relief diversity, average temperature in the breeding season, the proportion of wetlands and the density of street networks had the strongest impacts on most species (Tab. 4). At least one of these variables was important for all species – except for Red Kite, which was primarily influenced by the proportion of grasslands, woody edge structures and the proportion of deciduous trees in the landscape. Although not selected as important variable for all species, breeding-season average temperature generally had a strong positive impact on most species, except on Montagu's Harrier, while breeding season average precipitation generally showed a negative impact, except on Red Kite. Relief diversity also had a strong impact on most species with positive effects on relief/settlement species and negative effects on all other species that are largely confined to lowlands in Germany. Although being distributed in lowlands in Eastern Germany, a certain relief diversity seems to allow for higher occurrence probability of Osprey within its distribution range.

The proportion of settlements, wetlands, open land, grasslands, woody edge structures and tree species diversity was selected in all species for which these variables were included in initial model runs. Some of these variables had strong impacts on species' occurrence probabilities (Tab. 4). Wetlands provide important habitats not only for wetland species, but also for Marsh Harrier and Black Kite as well as Eurasian Hobby known to breed and feed in vicinity to such sites. As expected, settlements provided important habitats for building/relief-breeders (Eurasian Eagle-Owl and Peregrine Falcon) and White Stork breeding within or at edges of built-up areas, but settlements were largely avoided by most other species. Similarly, high densities of roads and streets were avoided by most species, while White Stork seemed to benefit from both categories and Black Kite from a certain density of roads as well. The effect of open land was mainly quadratic, indicating a certain optimum of available open land for most species except for Peregrine Falcon, White-tailed Eagle and Montagu's Harrier. The latter is strictly confined to breeding in arable landscapes resulting in a strong positive effect of open land, while White-tailed Eagle and Peregrine Falcon breed within landscapes dominated by forests or settlements, explaining the negative effect of open land on these two species. A high proportion of grasslands was especially important for bird species primarily using open land as well as for Eurasian Hobby. Woody edge structures showed strong impacts especially on those species breeding at forest edges (e.g. Red and Black Kite) as well as within forests (wetland species and building/relief species). Environmental variables describing land use practices, intensity or diversity of land use generally showed weaker effects than broad-scale patterns in land-cover across Germany.

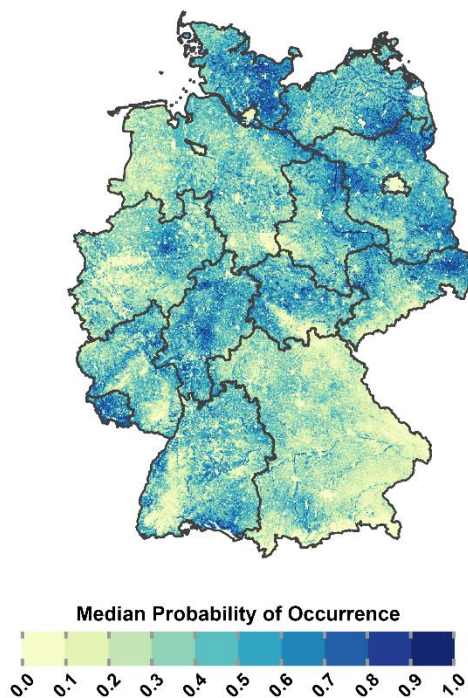
Interactions between variables often revealed a more nuanced picture of the impacts of environmental parameters on a species' occurrence probability (Tab. S4). Strong interactions were apparent for the proportion of open land, grassland and woody edge structures with a variety of other environmental parameters. Especially, the proportion of open land interacted with effects of other parameters (e.g. settlements, wetlands, grasslands, woody edges, soil quality). For example, a strong interaction of open land with the proportion of settlements was apparent for all farmland species. The interaction indicates that occurrence probability decreased with increasing proportion of settlements if a high proportion of open land is available, but effects of settlement proportion were negligible or positive (White Stork) in landscapes with low availability of open land, that are generally avoided by these species. White Stork however also seems to reach high levels of occurrence probability in landscapes with low proportion of open land, if sufficient nesting sites within or at the edges of settlements are available.

Aggregation across species

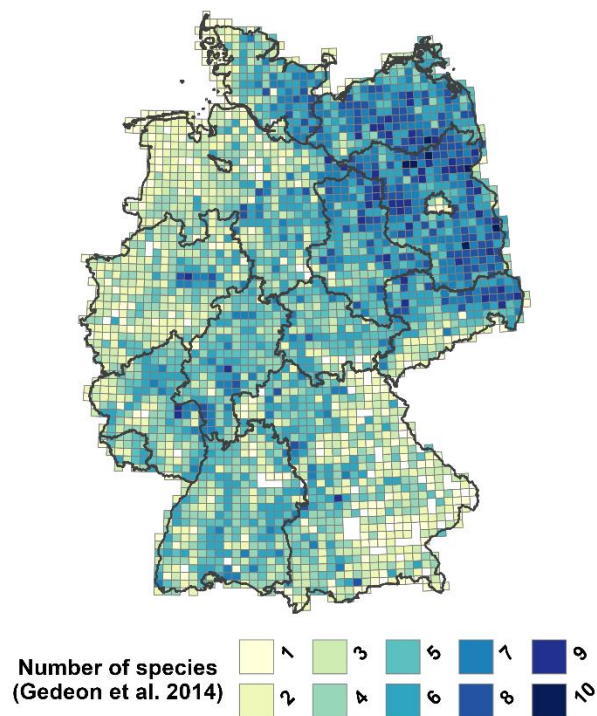
Median occurrence probability across species revealed similar patterns compared to the aggregated number of species occurrences according to Gedeon et al. 2014 (Fig. 1). The patterns of the species distribution in the aggregated model map (Fig. 1A) correspond broadly to the distribution of species according to Gedeon et al. 2014 (Fig. 1B). In particular, similar "hotspots" or distribution centres emerge. This indicates that the fine-scaled model predictions can replicate the broad-scale distribution patterns of the considered species and underlines the robustness of the approach. However, differences in the two distribution maps are also apparent, likely owing to temporal differences between the data sources, population dynamics or differences in spatial resolution.

Fig. 1: Aggregation of species-specific predictions. The normalised median A) probability of occurrence and C) the deviation from the mean (standard error) and D) median habitat suitability are shown. Aggregated species occurrence for 2005-2009 according to the Atlas of German Breeding Birds Gedeon et al. (2014) is shown in B) for comparison.

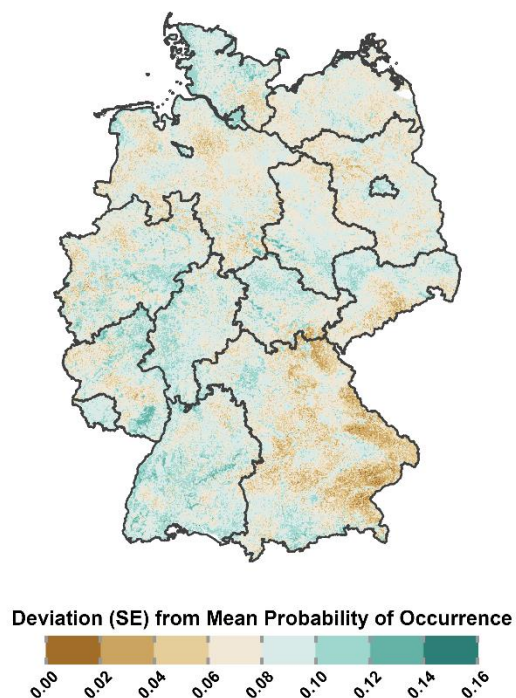
A



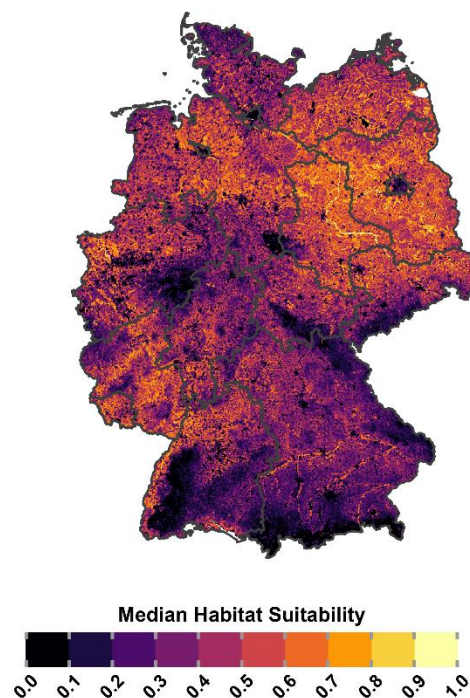
B



C



D



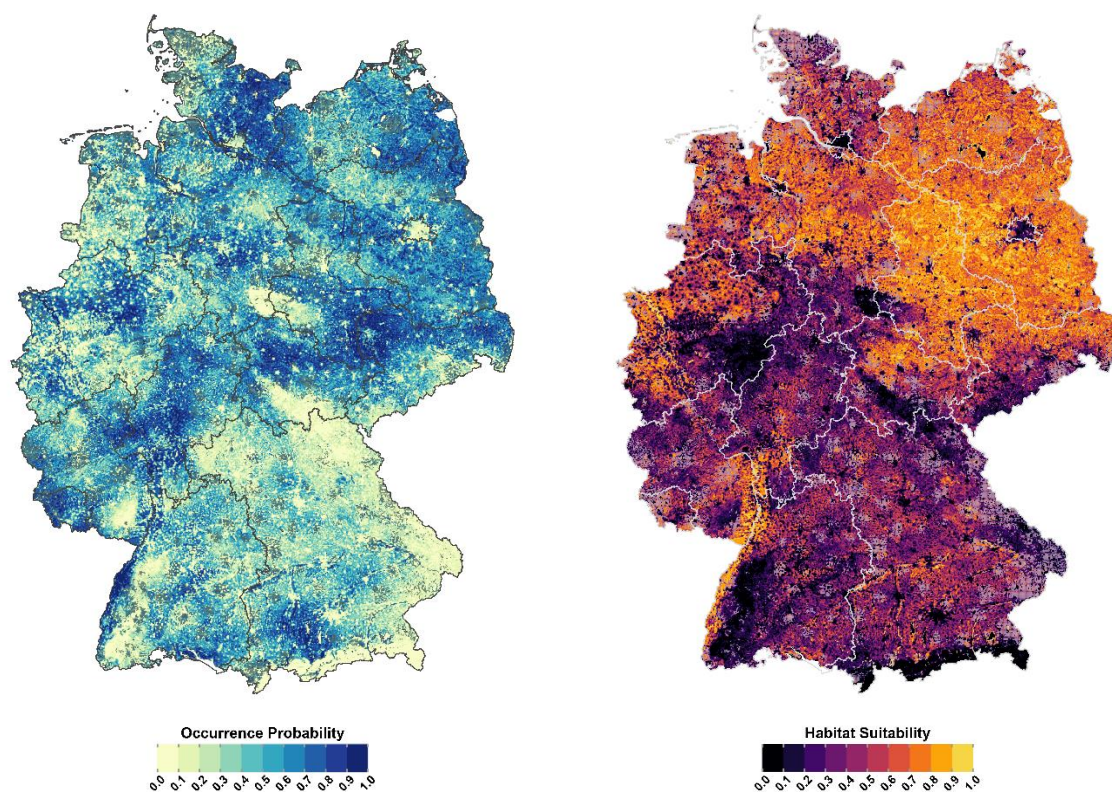
As species requirements and distributions across Germany vary considerably, deviation from the mean probability of occurrence also differs across landscapes in Germany (Fig. 1C). Here, areas emerge in which the probability of occurrence does not vary greatly between species, especially in areas with a low probability of occurrence of all species. However, areas with greater differences between species also stand out (e.g. Palatinate Forest). To identify potentially suitable habitats or landscapes with suitable habitats across all species, we also determined the median habitat suitability (Fig. 1D).

Uncertainty in model predictions

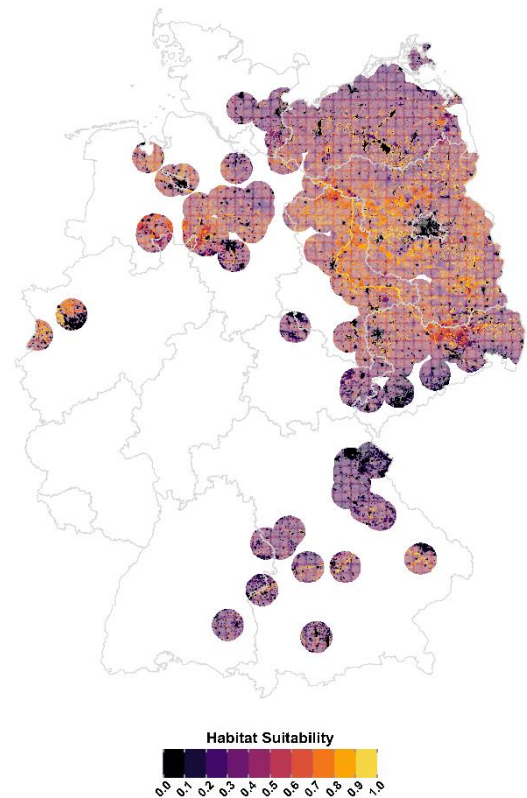
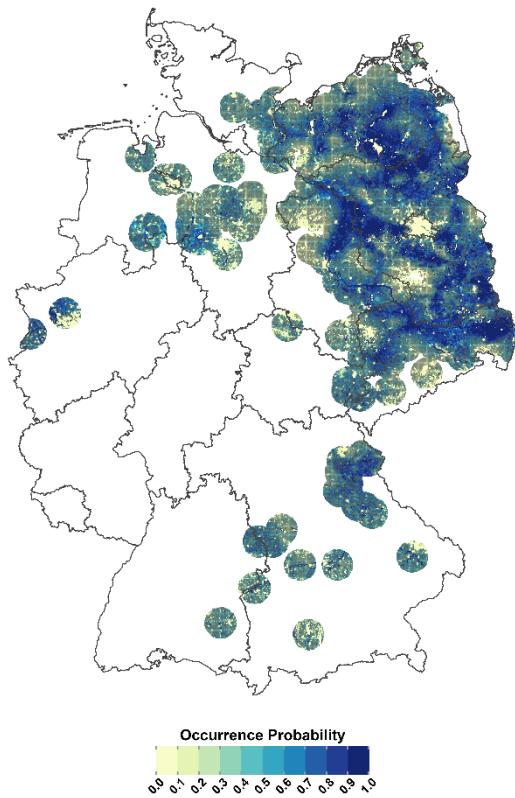
The uncertainty of predicted habitat suitability and occurrence probability varied considerably between species and regions in Germany. Using models allows to quantify these uncertainties precisely and they need to be taken into account when interpreting or using the resulting model maps. The species-specific maps therefore visually highlight areas with high uncertainty (range between confidence intervals (CI) > 0.4) that should be interpreted with caution (Fig. 2). However, depending on the intended purpose, different approaches should be chosen with care to filter out or propagate uncertainty of the model predictions. In most cases, areas with high uncertainty occur where data availability on occurrence data is low. This may be attributable to several, possibly interacting reasons such as lacking sources on data, low breeding density of the species (e.g. in Black Kite for north-west and south-east Germany) or because effects of dominant environmental conditions so far cannot be reliably estimated for some species. Uncertainties may also prevail in regions where specific combinations of environmental conditions are hardly covered by existing presence-absence data.

Fig. 2: Model predictions of occurrence probability and habitat suitability per species. High uncertainty in predictions (CI range > 0.4) is depicted by grey and white overlays in maps of occurrence probability and habitat suitability, respectively. Predictions for Osprey and White-tailed Eagle were limited to 20km around presence points as the species are not distributed nationwide in Germany.

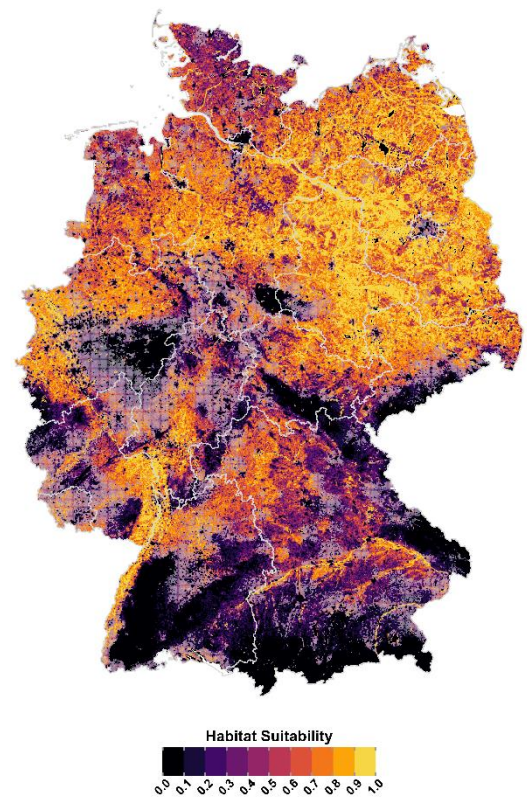
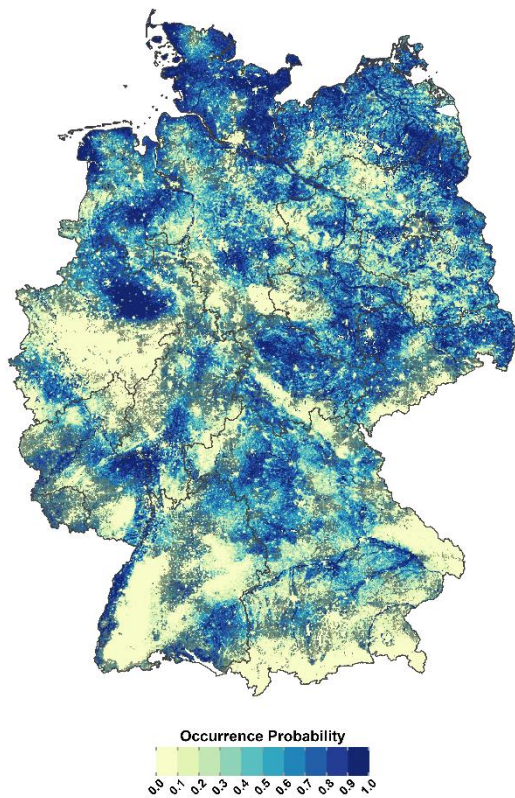
Eurasian Hobby



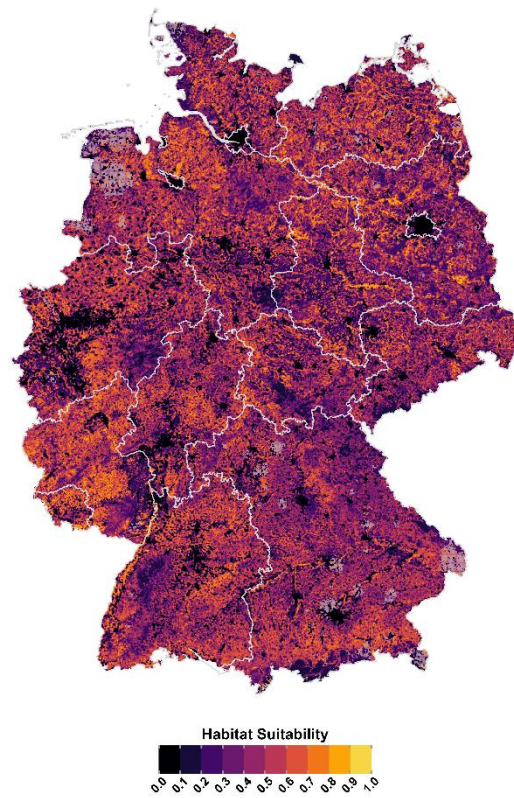
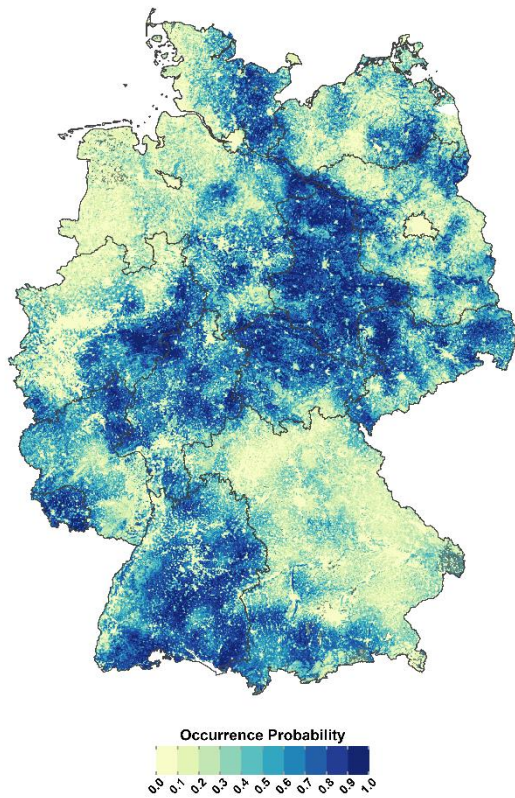
Osprey



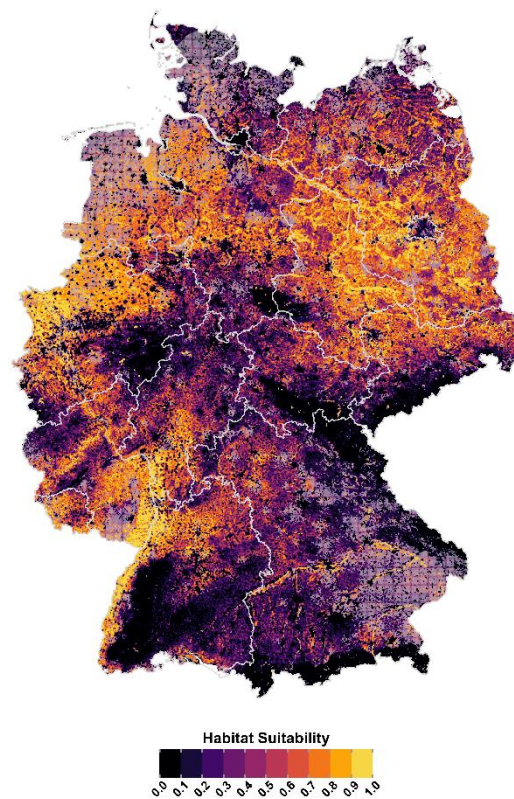
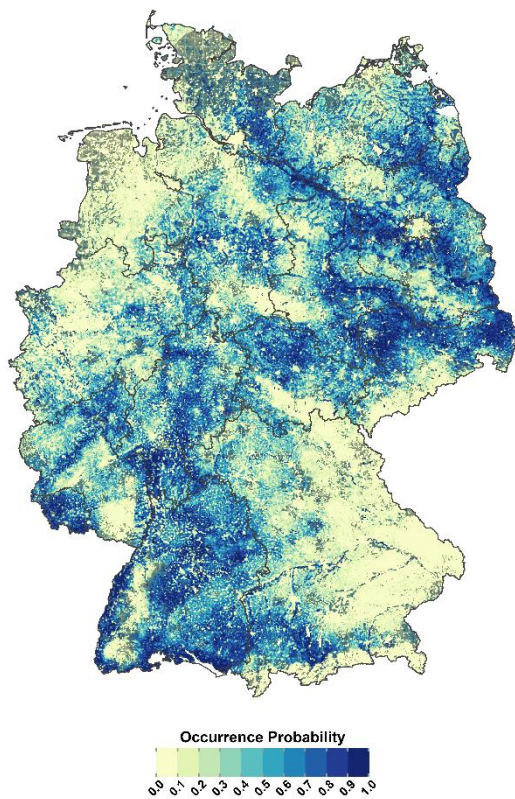
Marsh Harrier



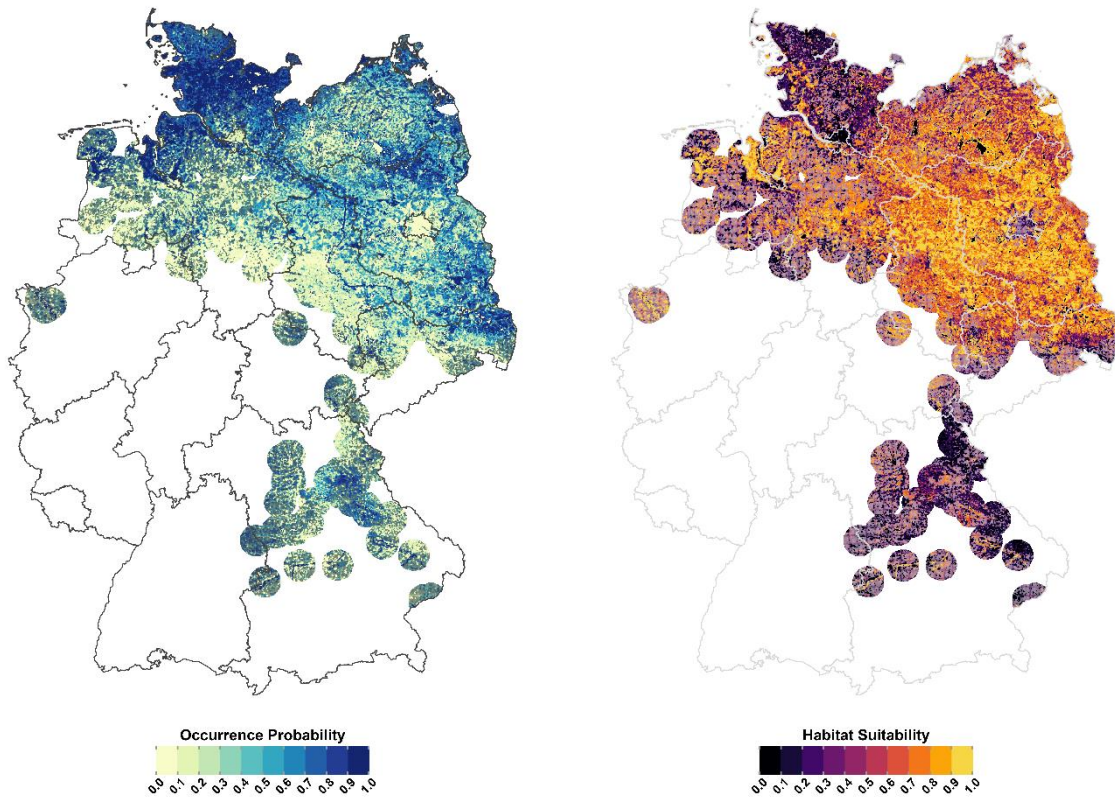
Red Kite



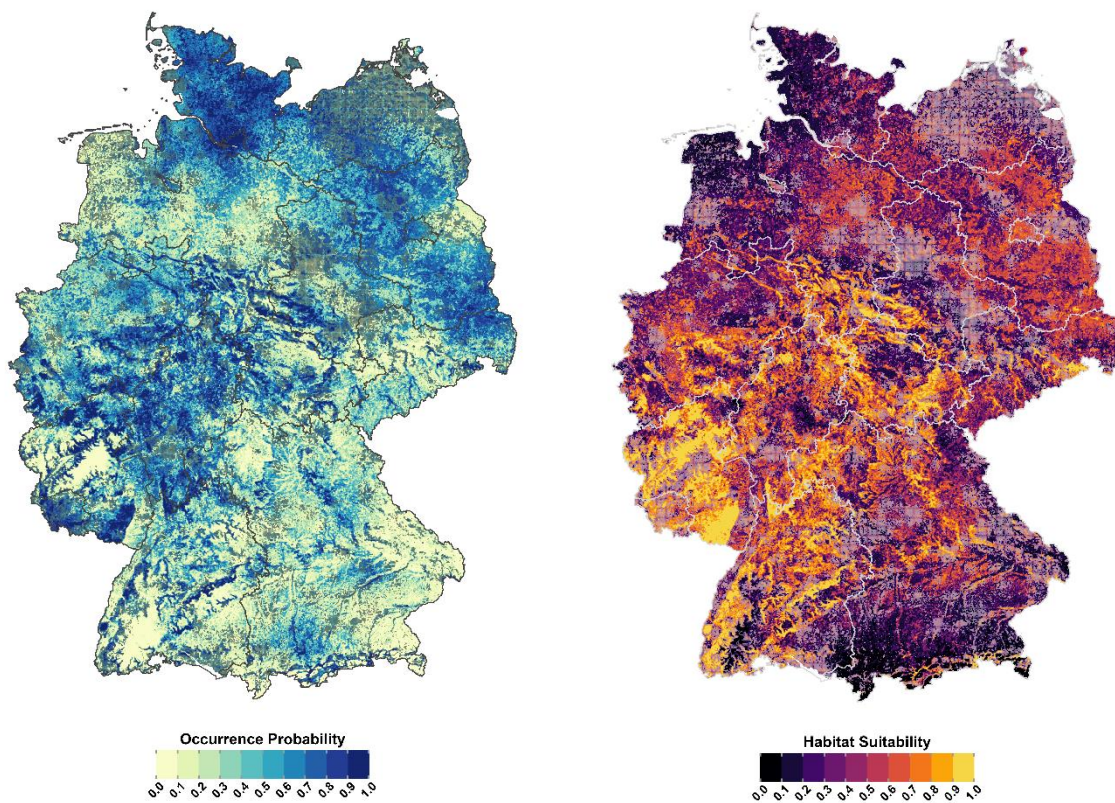
Black Kite



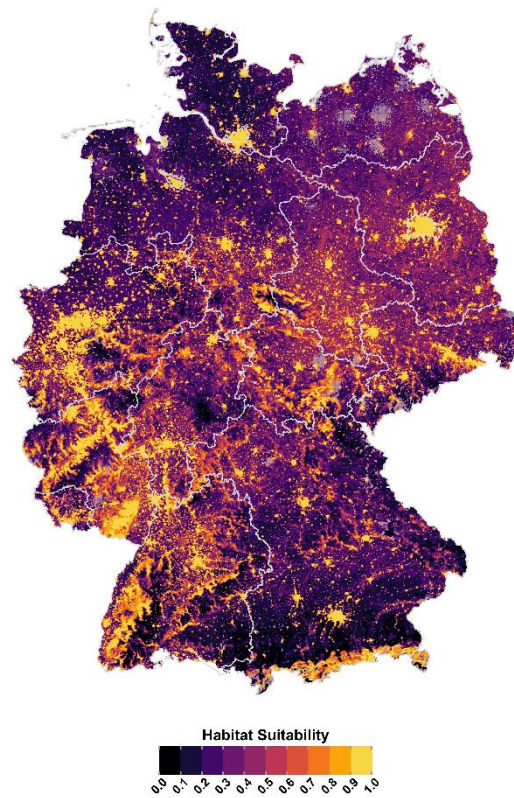
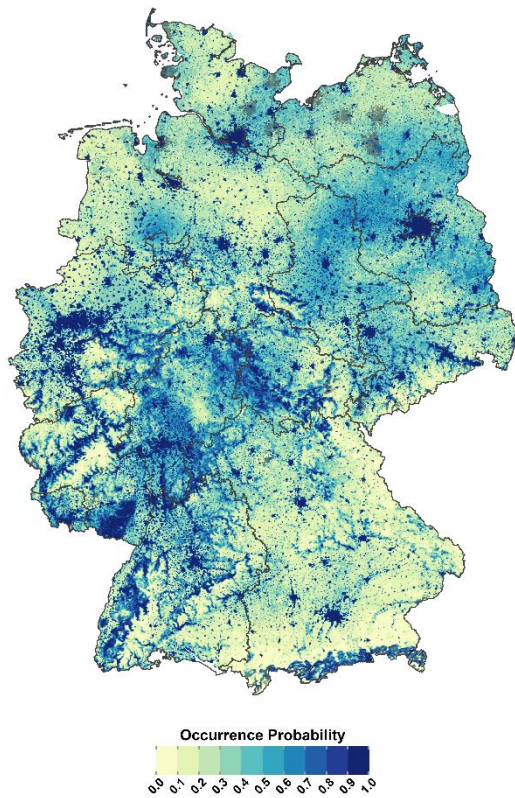
White-tailed Eagle



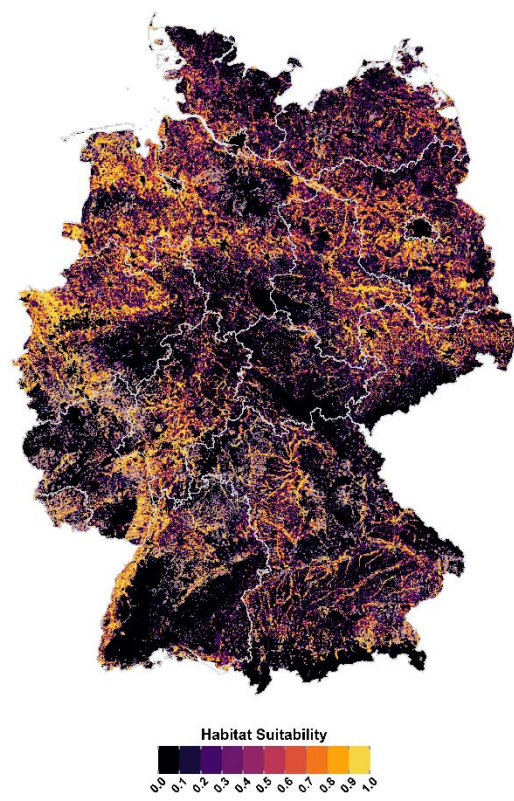
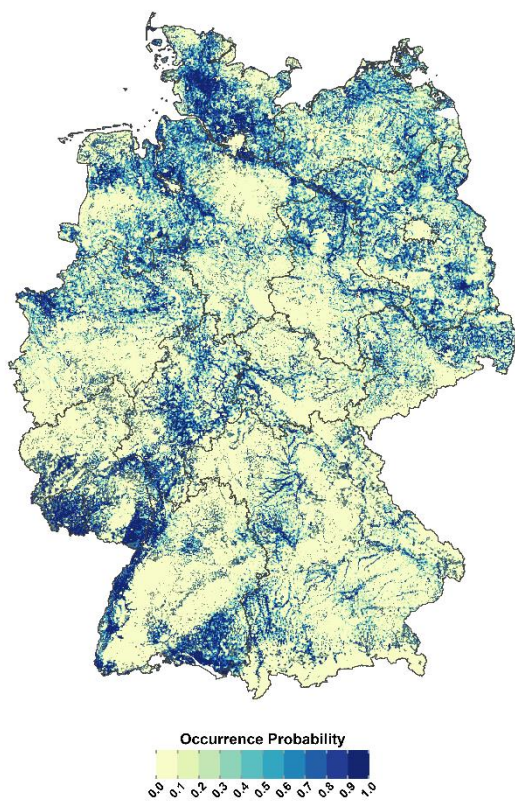
Eurasian Eagle-Owl



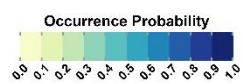
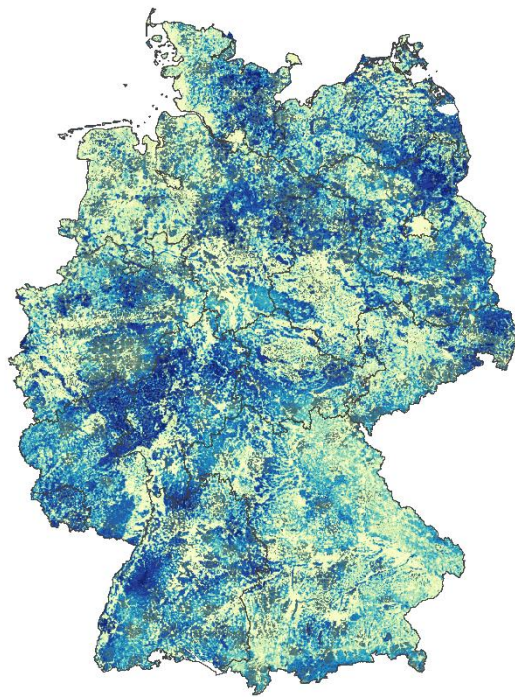
Peregrine Falcon



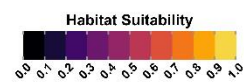
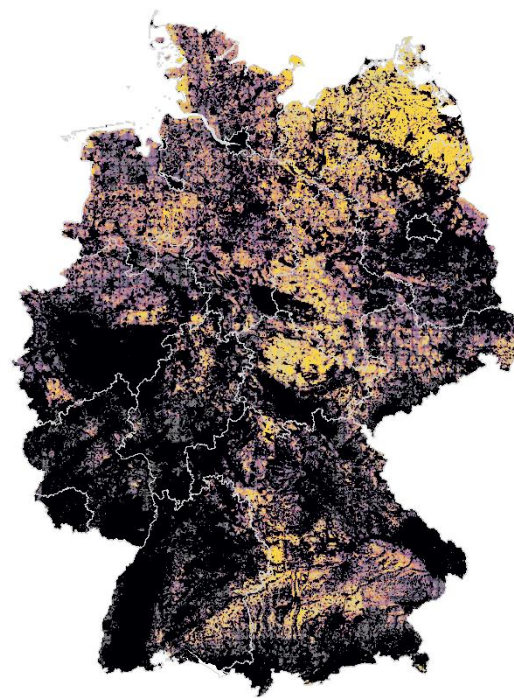
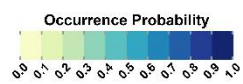
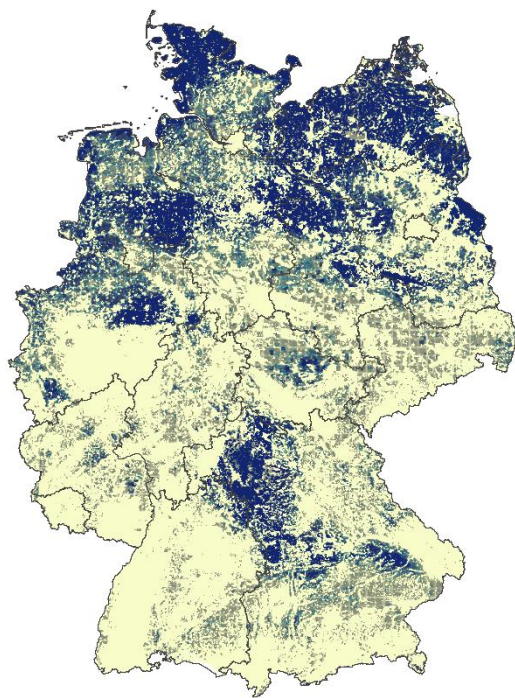
White Stork



European Honey-Buzzard



Montagu's Harrier



Discussion

Based on our approach to combine heterogeneous occurrence data from different sources with hierarchical distribution models we present comprehensive and up-to-date information on the nationwide breeding distribution of eleven large-bodied bird species in Germany. With the model predictions we integrate the effects of environmental drivers as well as intrinsic population dynamics for comparison across regions and federal states and provide details at high-resolution. The results show good quality in validation and reproduce the known broad-scale distribution of the selected bird species in Germany from the last Breeding Bird Atlas (Gedeon et al., 2014). Thus, we are confident that they convey useful and robust information to support further actions for enhancing the protection of these species under expanding wind turbine construction in Germany.

By using the model predictions, areas of high occurrence probability and habitat suitability can be delineated for each species and across species. The resulting maps provide the basis for identifying areas with high potential for effective implementation of conservation measures and allow a large-scale prioritisation for the national species recovery programmes. The maps could also be used within regional planning processes, especially in the context of renewable energy expansion. Here, probability of occurrence as well as habitat suitability for these species may fill gaps at sites where current data on species occurrence is unavailable or highlight areas with further need for data collection. Subsequently, targeted field surveys could be carried out to gain certainty about species occurrence, especially if the uncertainty of model predictions is high. For example, the model results for Eagle-owl show substantial uncertainty in several coastal and inland areas where occurrence data are lacking but habitat suitability varies (Fig. 2).

We stress here that modelling results generally contain an inherent uncertainty that may vary between species as well as in space and time. This can complicate the use of such data in practice; however, it helps to clearly address the possibilities and limitations – often also more straightforwardly than with other types of information like expert elicitation or field surveys of varying intensity. We provide the uncertainty of our model predictions in figures and as data layers and underline the need to consider these adequately for further use (e.g. by highlighting areas with high uncertainty for mapping or by propagating the precision of estimates in modelling approaches).

Based on our work, we provide the current version of the model results for public access and applications in relevant context. Since our project is ongoing, we advise that further development may lead to differences with future versions and highlight the importance for users to also reference the version history (current v.1.0) for their applications. With the chosen approach we have established a flexible modelling platform to incorporate heterogeneous data from different sources. This also allows future updates of the models if new occurrence data or other geospatial variables become available. Yet, the explanatory power of the results is currently limited to the eleven bird species considered and, clearly, expanding energy infrastructure construction has the potential to impact many more. When using the model predictions, it is therefore also important to evaluate if the reflected habitat preferences and occurrence patterns are suitable choices for the questions at hand.

Methodical considerations

The strength of the chosen modelling approach is that survey data and casual observations of different origin and intensity can be unified to a common framework. Thereby, occurrence data from different years and regions as well as environmental variables at varying resolution and timeframes are used to gain an understanding of the probability of species occurrence. In the present state of widely heterogeneous data availability on biodiversity and its changes over time, this also means that some limitations remain until better coverage, data management and standardisation are achieved. With regard to the breeding bird distributions of the considered species, our models currently provide the most comprehensive nationwide information. Until new atlas surveys become available, which can also describe species abundance in comparable ways, our models will remain the most reliable source of data.

While collating data and running the models, the available information was checked carefully and expert knowledge on species ecology and distribution was considered as far as possible. The aim of the project was to generate results for as many as possible of the 15 bird species listed in the Federal Nature Conservation Act and combine these to an aggregated data layer for Germany. Discussing the estimated effects and model predictions for individual species requires additional effort (see Katzenberger 2019) and we do not go into such detail here. For species specific usage of our results, we advise users to critically examine if the data layers and effect sizes considered reflect the questions at hand. For some species and regions, we noticed imbalances in the data basis, that are counteracted to some degree by the models. Yet, with the present state of information, it can be difficult to judge small scale occurrence patterns and potential bias in the results. Little information on species occurrences was available for parts of north-east Germany in Mecklenburg-West Pomerania (noticeable for White-Tailed Eagle but likely other species as well), as well as for eastern and north-western Bavaria, central Rhineland-Palatinate and north-western Lower Saxony. In addition, results for Osprey currently suffer from high uncertainty in many areas which need further investigation.

Since the intensity of grassland use and mowing events can be important for breeding and foraging bird species, we also considered newly available remote-sensing products for grassland mowing events (Schwieder et al., 2021). Because of better spatial consistency and less visible satellite artefacts, we used the median date of the first cut for modelling, which correlates with the total number of mowing events. However, this metric may also be confounded with broad-scale land-use management and grassland phenology, so it could be more appropriate to use a relative metric here, for example with a local moving window approach.

When collecting breeding occurrence data of relatively rare bird species, the national scale is useful, or even necessary, for gaining suitable sample sizes to estimate more complicated multivariate models and derive spatial correlation patterns. Yet, for some species habitat preferences and external anthropogenic drivers may vary regionally. For example, Red Kites prefer forest edges as breeding sites in some regions but smaller treelines and woodlands in others (Hartmann et al., 2023; Walz, 2014), or Marsh Harriers mainly choose wetlands and grasslands in coastal or riverine areas for breeding, while inland agricultural fields are often selected as nest sites (Gedeon et al., 2014). By applying nationwide models, such differences are drawn towards the mean of an overall effect size, unless specifically accounted for. The spatial dependency component in the selected modelling approach does reflect such regional differences to some

extent – however unseparated from a variety of potential other factors. It may therefore be a promising extension of the current approach to explicitly include regional differences in the estimation of covariate effects. This may be achieved by including interactions for regional clusters or explicit random effects on covariates within the flexible hierarchical structure (Anderson et al., 2024).

To assess the quality of the model fit, we currently use a simple random split for training and testing data sets. But, when modelling spatial data, inherent autocorrelation can negatively impact validation statistics, which can be overcome by tailored spatial clustering in validation blocks (Roberts et al., 2017; Valavi et al., 2019). We explicitly consider spatial dependency in the model predictions; yet, validating models with blocking can also better account for the entire multivariate environmental space and thus validation statistics of our models will be refined accordingly in a next step.

Remarks for using the model results in practice

When using the model predictions for single species or aggregated across all species, several points need to be considered. The maps describe how likely it is that breeding occurs in each raster cell, considering both the environmental drivers and large-scale distribution patterns (probability of occurrence) or alternatively only the effects of climate and landscape characteristics (habitat suitability). The population density or abundance cannot be estimated with the chosen models and the heterogeneous data availability currently hinders reliably calculating this nationwide.

The modelling results clearly show that extensive and standardised field surveys are necessary to gain a complete picture of the nationwide breeding distribution of such large-bodied bird species, since environmental variables can typically explain only a varying proportion of the variability. Our models integrate the currently best available knowledge from different data sources to a comparable picture. But on the local or regional scale more information from comprehensive field surveys or high-quality casual observations may be available and these need to be consulted in comparison - depending also on the intended use (e.g. necessary when considering wind turbine siting but more optional if optimising local habitat quality).

For practical use it is important to consider that the predictions cannot exactly pinpoint the breeding locations for individuals or pairs but rather give relative information, where these are more or less likely. In the absence of detailed and current field observations, this is the best information available, and it should be used if model uncertainty is not too high. The precision of the results can be judged by the standard error, where it is likely that the local probability falls within, or by confidence intervals, where the likelihood is very high that the probability is contained within. In cases with controversial findings from different sources or generally high uncertainty, the model results can be used as guidance where to survey preferentially to gain more reliable information.

Data availability

We provide all supplementary files via Zenodo: doi.org/10.5281/zenodo.13237339

Acknowledgments

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