LIFE AEGYPIUS RETURN

REPORT

Deliverable 2.1. Habitat suitability analysis for the Cinerous Vulture in Portugal and western Spain.

July 2024

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Almost four decades after becoming extinct in Portugal as a breeding species, the Cinereous Vulture (*Aegypius monachus*) returned to colonize the country in 2010, as some birds coming from Spain nested in the Tejo International Natural Park. Thanks to the conservation efforts carried out in both countries by NGOs and government entities, the number of breeding pairs has been steadily increasing. However, the Portuguese population is still too fragile, and its future remains uncertain. The LIFE Aegypius Return project will ensure the definitive return of the species.

https://4vultures.org/life-aegypius-return/

Coordinating beneficiary

VCF VULTURE CONSERVATION FOUNDATION

Associated beneficiaries

Palombar Associação de Conservação da Natureza e do Património Rural

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LPN - Liga para a Protecção da Natureza
Palombar - Conservação da Natureza e do Património Rural
SPEA - Sociedade Portuguesa para o Estudo das Aves
VCF - Vulture Conservation Foundation

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Herdade da Contenda, at SPA Mourão/Moura/Barrancos ©VCF

Abstract

Quantifying habitat use is crucial for understanding how animals fulfil their survival requirements and for informing conservation planning. The LIFE Aegypius Return project aims at consolidating Cinereous Vulture (*Aegypius monachus*) populations in Portugal and Western Spain. The Cinereous Vulture, an apex scavenger of conservation concern, is widely distributed across Eurasia but currently faces threats from anthropogenic mortality, changes in food resources, habitat loss and human disturbance. In this study, we employed penalized logistic regression to identify species-habitat associations and predict habitat suitability across the project area. Our Species Distribution Model (SDM) indicated that Cinereous Vultures select breeding sites characterized by evergreen forest patches on slopes with low levels of human disturbance. Additionally, the proportion of open areas and livestock density within a 40 km radius of the nest positively influenced breeding occurrence. Our species-habitat model identified four main fragmented patches of highly suitable habitat: (i) Serra Algarvia in Portugal, (ii) Sierra Pelada with discontinuous patches extending eastward to Sierra Morena, (iii) an area extending from Serra de S. Mamede to Tejo Internacional Natural Park in Portugal, and Sierra de San Pedro in Spain, connected to Serra de Malcata in Portugal and Sierra de Gata in Extremadura, and (iv) an area covering Parque Natural de Arribes del Duero in Spain and several Natura 2000 sites in Northern Portugal: Vale do Côa, Douro Internacional e Vale do Águeda, Rios Sabor e Maçãs, and the Eastern part of Montesinho/Nogueira. The modelled habitat estimates provided herein are a valuable tool for guiding monitoring efforts and conservation actions aimed at promoting the expansion of the Cinereous Vulture population in Portugal within the framework of the LIFE Aegypius Return project.

1. INTRODUCTION

The Cinereous Vulture is an apex scavenger whose global populations experienced a significant decline during the 20th century. The species became extinct in numerous countries due to various anthropogenic pressures, including habitat loss, mass poisoning from carnivore eradication campaigns, and direct persecution. At its historical lowest point, only two subpopulations remained: a western subpopulation in Spain and a small eastern subpopulation in north-east Greece (Cramp & Simmons, 1980). In 2004, the IUCN reclassified the conservation status of the Cinereous Vulture to Near Threatened.

In the last decades, effective legal protection, the end of persecution and poisoning campaigns, and the implementation of targeted conservation measures including reintroduction programs have allowed the species to recover (Moreno-Opo & Margalida, 2014). New breeding populations have been established in France and in Bulgaria. The species is doing particularly well in Spain, with significant increases in the number of breeding pairs observed in the two largest breeding colonies in Europe, located in Extremadura: + 51% in Sierra de San Pedro and + 24% in the Monfragüe National Park since 2016 (Terraube *et al.* 2022). The population in Spain now reached +3000 breeding pairs (Terraube *et al.* 2022).

In Portugal, the breeding population of Cinereous Vultures was extirpated in the 1970s. However, the population growth in Spain and conservation initiatives aimed at supporting scavengers in both countries have facilitated the natural recolonization of Portugal, with individuals dispersing from proximate Spanish colonies. The establishment of the first breeding pair occurred in 2010, and the population has since exhibited continuous growth. By 2022, the breeding population had expanded from a few pairs in a single colony (Tejo Internacional) to 40 pairs across four colonies.

However, the natural recolonization process is both slow and limited due to the species' colonial behaviour and high philopatry, which inhibit recolonization in areas distant from established colonies. The breeding colonies in Portugal remain fragile, characterized by a small number of pairs, a highly restricted breeding range, and limited inter-colony connectivity. These factors render them susceptible to stochastic events such as fire and poisoning or potential increases in mortality rates linked to collisions or electrocution associated with energy infrastructures. Additionally, birds from the Spanish breeding colonies exhibit a lower probability of foraging in Portugal due to insufficient food resources and carcasses in that country, resulting from different livestock densities and carcass management regulations, thereby impeding dispersal towards potentially suitable areas in Portugal and hindering recolonization.

To ensure the long-term favourable conservation status of the Cinereous Vulture in Portugal, the LIFE Aegypius Return project aims to enhance habitat and foraging conditions, mitigate threats, bolster the population, and build national capacities. This initiative is supported by a robust transnational partnership comprising beneficiaries from both Portugal and Spain, focusing on the recovery of the species in the border region of Portugal. This recovery effort is heavily reliant on and facilitated by the connectivity with the Spanish population.

The LIFE Aegypius Return project aims to release rehabilitated birds in the northernmost Portuguese breeding colony and implement habitat and food management actions to potentially attract wild birds to the study area. Consequently, these individuals are expected to occupy territories and establish breeding colonies in new areas with suitable habitat along the Spain-Portugal border. To identify these areas and guide subsequent conservation actions, we developed a predictive habitat suitability map using Species Distribution Modelling (SDM). SDMs are predictive spatial models that infer species-habitat associations by correlating species presence points with habitat covariates representing the species' optimal conditions and resources (Guisan, Thuiller, & Zimmermann, 2017; Matthiopoulos, Fieberg, & Aarts, 2020).

In this study, we utilized SDMs calibrated with remote sensing covariates and presence background data for the Cinereous Vulture in Portugal and Western Spain to predict habitat suitability across the project study area.

2. MATERIAL AND METHODS

2.1. Project study area

The LIFE Aegypius Return project intervention area is mostly comprised of 10 Special Protection Areas (SPA) in the border region of Portugal (7) and Spain (3) which already have Cinereous Vulture breeding colonies, or that apparently present adequate habitat for the species' expansion (Fig. 1) :

PTZPE0038 Douro Internacional e Vale do Águeda
PTZPE0037 Rios Sabor e Maçãs
PTZPE0039 Vale do Côa
PTZPE0007 Serra da Malcata
PTZPE0042 Tejo Internacional, Erges e Pônsul
PTZPE0045 Mourão/Moura/Barrancos
PTZPE0047 Vale do Guadiana
ES0000202 Campo de Azaba
ES0000370 Sierra de Gata y Vale de Pilas
ES0000434 Canchos de Ramiro y Ladronera

As the project aims at promoting connectivity among colonies through a variety of targeted conservation actions, within the project's scope a buffer area of 40 km to each side of the North-South Portuguese-Spanish border is generally considered as "the project area" (Fig. 1). This buffer radius was determined considering the average distance from the nest in which Cinereous Vultures usually search for food during the breeding season.

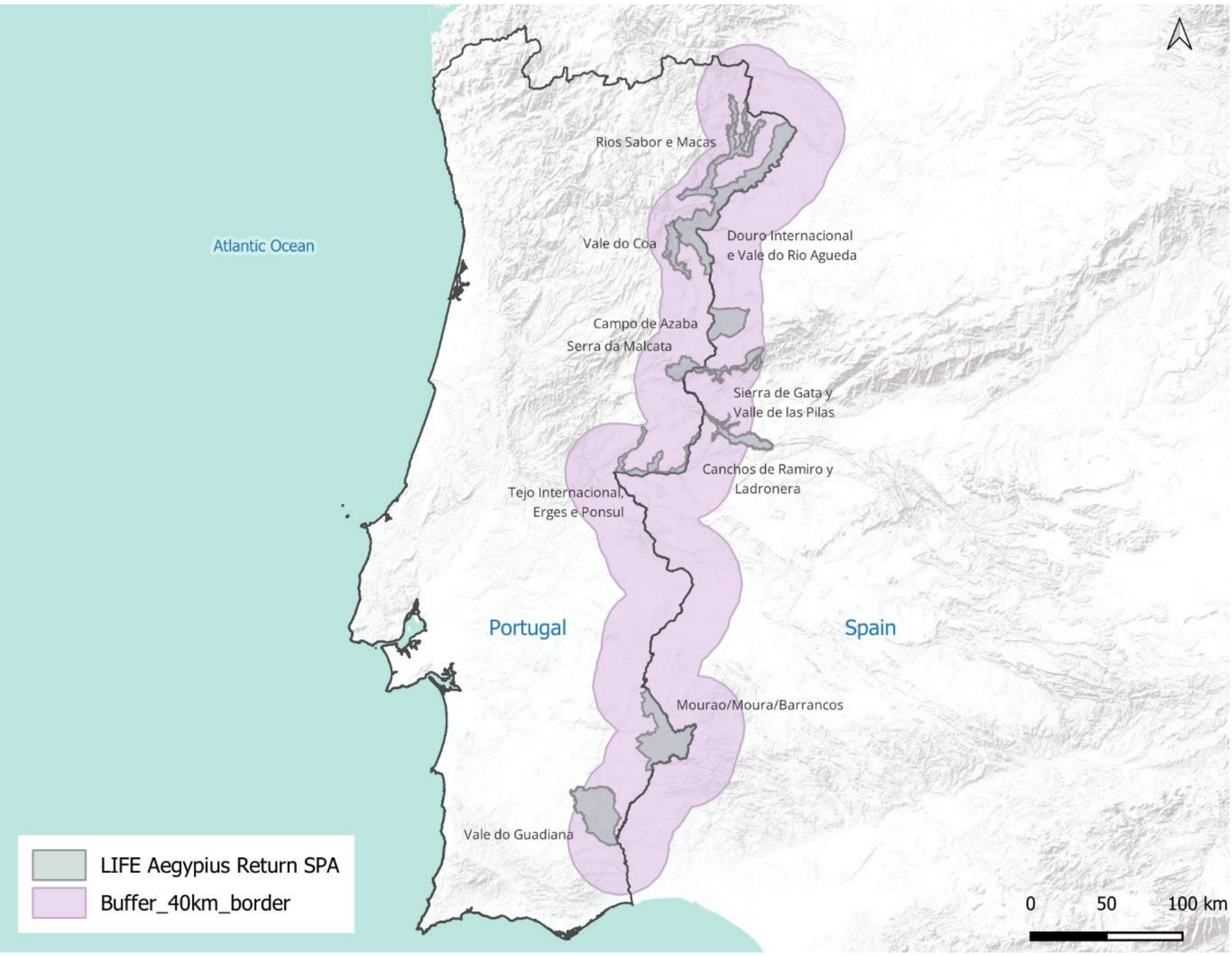

Fig. 1. Target Special Protection Areas (SPA) and LIFE Aegypius Return « project area » – a buffer of 40 km to each side of the North-South Portuguese-Spanish border considered for consolidating and expanding the Cinereous Vulture population in Portugal and Western Spain.

2.2. Species locations

For this study, Cinereous Vultures point localities included presence-only data consisting of nest locations (n=525) obtained through the monitoring of breeding Cinereous Vulture populations conducted by the project partners and statutory nature conservation authorities across the study area, in Portugal and Spain (Fig. 2).

Nest locations initially included data from two Spanish nuclei: i) Andalusia (n=149); ii) Extremadura (n=247); and 4 Portuguese nuclei: iii) Contenda (n=22); Douro (n=6); iii) Malcata (n=16) and Tejo International (n=85). We then applied a spatial filter using the spThin package, resulting in a single occurrence in each 1-km raster grid cell. The thinned occurrence dataset resulted in a filtered subset of 145 occurrence records for the Cinereous Species distribution model. We employed spatial filtering as it offers the most efficient approach for addressing sampling bias (Kramer-Schadt *et al.*, 2013; Boria *et al.*, 2014) and potential spatial autocorrelation arising from the semi-colonial behavior of the study species and the close proximity of occupied nests within each subpopulation across the study area. Spatial autocorrelation can strongly affect the quality of SDMs and should not be ignored when producing occurrence maps (Guelat & Kery, 2018).

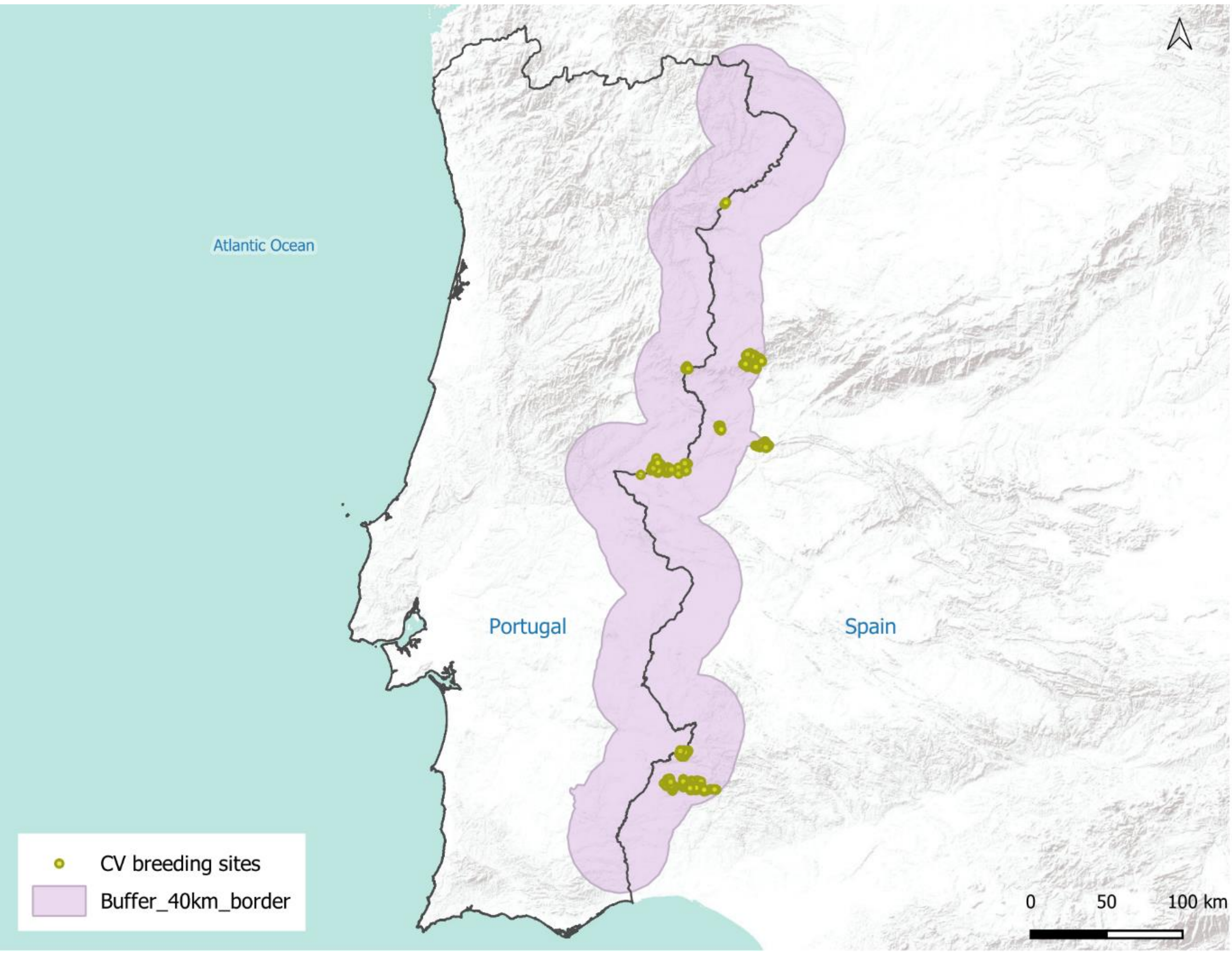

Fig. 2. Locations of Cinereous Vulture breeding sites from Portugal and Western Spain included in this study.

2.3. Environmental covariates

Ecological variables such as climate and habitat may drive species distribution at multiple spatial scales. Overall, climate mostly influences th e distribution of species at rather large-scale while habitat factors may influence breeding site selection at several spatial scales (Pearson and Dawson, 2003): at fine scale in the case of characteristics of the immediate environment around the nest or at larger scale if these factors are related to foraging habitat quality. Consequently, we extracted environmental variables at three different scales: i) 1km for habitat variables directly related to fine-scale breeding habitat selection (topography, tree cover density, human disturbance); ii) 10km for climate variables; and iii) 10, 20 and 40 km for environmental variables related to foraging habitat selection considering the average foraging distance recorded from GPS-tagged Cinereous Vultures in other studies (Rousteau, T. *pers. comm*).

All variables were built at 1km resolution in Lambert azimuthal equal area (LAEA) projection (epsg:3035) using R software ("R version 4.3.1 (2023-06-16)"). See Table 1 for a summary of bioclimatic and habitat variables.

2.2.1. Bioclimatic variables

We extracted a set of 8 bioclimatic variables that have previously performed well when modelling bird distributions (Barbet-Massin *et al.*, 2009) and that have a potential impact on vulture reproductive success. WorldClim variables are generated through interpolation of average monthly weather station climate data from 1970 to 2000.

We extracted the following bioclimate variables for subsequent use in the Species Distribution Model: i) Annual mean temperature; ii) Temperature seasonality; iii) Maximum temperature of the warmest month; iv) Minimum temperature of the coldest month; v) Annual precipitation; vi) Precipitation of wettest month; vii) Precipitation of driest month; viii) Precipitation seasonality.

2.2.2. Topography

Landscape structure can affect flight conditions for large soaring raptors and the energy expenditure needed to perform repeated movements between the nest and foraging grounds. Nest orientation can also impact microclimate conditions and thus chick survival during the first weeks when they are most vulnerable to adverse weather conditions.

In addition, landscape structure around breeding sites is also associated to their accessibility and vulnerability to anthropogenic activities. Cinereous Vultures are often found on slopes in rugged areas. We extracted five different topographic variables at 1km resolution: i) elevation; and from the elevation, four other variables were derived: ii) slope; iii) eastness; iv) northness (these two indices of northness and eastness provide continuous measures (–1 to +1) describing orientation of the slopes).; and v) ruggedness.

2.2.3 Landscape composition and food availability

The three following habitat covariates are related to breeding habitat quality at the site scale (1km).

a) Canopy cover

Percent canopy cover was obtained from the Tree Cover Density (TCD) map for 2018 available at 100m per pixel resolution in LAEA projection (downloaded from https://land.copernicus.eu/pan-european/high-resolution-layers/forests/tree-cover-density/status-maps/2018). We resampled it at 1 km resolution using the bilinear method and calculated the percent canopy cover with the focal function.

b) NDVI from December to February

Since Cinereous Vultures mainly use evergreen tree species (Morán-López *et al.*, 2006a), we calculated a NDVI (normalized difference vegetation index) during the pre-laying period (December to February) to "map" a proxy of the available supports for the nest during winter when pairs settle on their breeding site. For this purpose, we used Google Earth Engine to extract NDVI rasters from MOD13Q1.061 Terra Vegetation Indices 16-Day Global at 1km, from December to February for each year during the period 1999-2019. Values were then averaged for the whole study period and reprojected at the reference grid resolution using the bilinear method.

c) Human Footprint index

The Human Footprint Index (HF3-1) provides a global map of the cumulative human pressure on the environment from 2000 to 2020, at a spatial resolution of 300 m (downloaded from the Wildlife Conservation Society website: https://wcshumanfootprint.org/data-access). The human pressure is measured using eight variables including built-up environments, population density, electric power infrastructure, croplands, pasture lands, roads, railways, and navigable waterways. We projected this map to match the reference grid at 1km resolution in LAEA projection and calculated the average index at the breeding site scale in a radius of 1km with the focal function.

The three following habitat covariates are related to foraging habitat quality at the home range scale (10, 20, 40 km).

d) NDVI from February to August

Morant *et al.* (2023) have demonstrated that the availability of wild ungulate carrion from natural sources and big game hunting is greater in more productive regions, as indicated by higher NDVI values, in Spain. Wild ungulates and lagomorphs constitute a significant portion of the Cinereous Vulture's diet. However, fine-scale data on the abundance of these species across the study area are often unavailable for consistent time frames and spatial extents. Consequently, this study utilizes NDVI indices as a proxy for assessing food availability for Cinereous Vultures during their breeding period. We also used Google Earth Engine to extract NDVI rasters from MOD13Q1.061 Terra Vegetation Indices 16-Day Global at 1km, from February to August for each year during the period 1999-2019. Values were then averaged for the whole study period and reprojected at the reference grid resolution using the bilinear method. We then calculated the mean NDVI in a radius of 10km, 20km and 40 km with the focal function.

e) Proportion of open habitat

Open habitats are actively selected by foraging Cinereous Vultures as they use visual cues to detect carcasses and their probability of detection is much higher in this type of habitat. Also, open habitats are associated with livestock breeding. Open areas were derived from CORINE Land Cover (CLC) map for 2018 available at 100m per pixel resolution in LAEA projection (downloaded from https://land.copernicus.eu/pan-european/corine-land-cover/clc-2012). We have reclassified the codes 231: Pastures, 321: Natural grasslands, 322: Moors and heathland, 323: Sclerophyllous vegetation, 324: Transitional woodland-shrub and 333: Sparsely vegetated areas by 1, 999: NO DATA and NA by NA and the rest by 0. Then we resampled at 1km per pixel resolution with the bilinear method and calculated the percent open areas in a radius of 10km, 20km and 40 km with the focal function.

f) Small ruminant density (number/km2)

We used The Food and Agriculture Organisation (FAO) data (Gilbert *et al.*, 2018) to calculate a density of small ruminants (sheep and goats) per km² as an indicator of potential livestock carrion supply.

The third version of the Gridded Livestock of the World (GLW) has a reference year of 2010 and includes global distributions of sheep and goats at a spatial resolution of 5 minutes of arc (approximately 10 km at the equator). These datasets contain the global distribution of sheep/goats in 2010 expressed in total number of sheep/goats per pixel. Data for cattle, sheep and goats are available at http://www.fao.org/livestock-systems/en/ and the GIS file of the area per pixel (square km; 4320 by 2160 pixels of 0.083333 decimal degrees resolution) is available at this link.

We used layers containing the DA animal numbers per pixel, with weight estimated by the Random Forest model. To obtain small ruminant density, the number of sheep (layer "5_Sh_2010_Da") and goats (layer "5_Gt_2010_Da") was first added together and then divided by the area of the pixel. We then projected these two maps to match the reference grid at 1km resolution in LAEA projection and calculated the mean density in a radius of 10km, 20km and 40km with the focal function.

We thus extracted a total of 25 environmental covariates that were used to predict Cinereous Vulture habitat across the study area (Table 1).

Table 1. List of environmental covariates extracted to predict Cinerous Vulture breeding habitat suitability across the study area.

Covariate name	Scale
Climate	
1-Annual mean temperature	10 km
2-Temperature seasonality	10 km
3-Max. temp of the warmest month	10 km
4-Min. temp. of the coldest month	10 km
5-Annual precipitation	10 km
6-Precipitation of wettest month	10 km
7-Precipitation of driest month	10 km
8-Precipitation seasonality	10 km
Topography	
9-Elevation	1 km
10-Slope	1 km
11-Eastness	1 km
12-Northness	1 km
13-Ruggedness	1 km
Landscape composition	
14-NDVI_Dec-to-February	1 km
15-Human Footprint Index	1 km
16-Canopy Cover	1 km
17-NDVI_Feb-to-August	10 km
18-NDVI_Feb-to-August	20 km
19-NDVI_Feb-to-August	40 km
20-Prop. of open habitat	10 km
21-Prop. of open habitat	20 km
22-Prop. of open habitat	40 km
23-Small ruminant dens.	10 km
24-Small ruminant dens.	20 km
25-Small ruminant dens.	40 km

Multicollinearity between environmental predictor variables can bias models by over-representing the biological relevance of correlated variables (Franklin, 2009; Phillips *et al.*, 2006). First, we performed a hierarchical ascendant classification with a distance metric based on Spearman's rank correlation coefficient to measure the correlation between environmental variables. When two or more variables had correlation values above a threshold of 0.7 (Dormann *et al.*, 2013), they were grouped together. This analysis demonstrated a strong correlation between habitat and food availability covariates extracted at 10, 20, and 40 km scales. Consequently, we opted to retain only NDVI_February-to-August, Proportion of open habitat, and Small ruminant density extracted at the largest scale, i.e. 40 km. The remaining 19 variables were then checked for collinearity using Spearman's correlation coefficient with only variables rs ≤ |0.7| retained for consideration as predictors, using the "corSelect" function in the R package fuzzySim (Barbosa, 2015, 2018).

Finally, 10 variables were selected: Temperature seasonality, Precipitation of the wettest month, Eastness, Northness, Elevation, Human Footprint Index, NDVI_Dec-to-Feb, Prop. of open habitat_40km, Small ruminant density and Slope. The 9 other covariates were excluded from the subsequent modelling steps.

All VIFs from remaining covariates were <5.

2.4. Species distribution model

Following the methodological approach developed in previous studies from Sutton *et al.* 2021, 2022, we parametrised the SDMs using a fine pixel grid (~1-km), equivalent to fitting an inhomogeneous Poisson process (IPP) with loglinear intensity (Baddeley *et al.*, 2010). We did this because the IPP framework is the most-effective method to model presence-only data (Warton & Shepherd, 2010), common to many raptor monitoring programmes which solely seek to identify occupied areas and monitor breeding sites (Geary, Haworth, & Fielding, 2018). We fitted SDMs using penalised logistic regression, via maximum penalised likelihood estimation (Hefley & Hooten, 2015) in the R package maxnet (Phillips *et al.*, 2017). Penalised logistic regression imposes a regularisation penalty on the model coefficients, shrinking towards zero the coefficients of covariates that contribute the least to the model, reducing model complexity (Gaston & Garcia-Vinas, 2011). We limited model complexity because this is necessary when the primary goal is to use SDMs for predictive transferability in space (Helmstetter *et al.*, 2021). The maxnet package fits the SDM as a form of infinitely weighted logistic regression (presence weights = 1, background weights = 100), based on the maximum entropy algorithm, MAXENT (Phillips *et al.*, 2017). MAXENT is designed for presence-background SDMs and is mathematically equivalent to estimating the parameters for an IPP (Renner & Warton, 2013; Renner *et al.*, 2015). We used a tuned penalised logistic regression algorithm because this approach outperforms other SDM algorithms (Valavi *et al.*, 2021), including ensemble averaged methods (Hao *et al.*, 2020).

We evaluated calibration accuracy for the Cinerous Vulture SDM using a random sample of 1450 background points as pseudo-absences (1:10 ratio) recommended to sufficiently sample the background calibration environment (Barbet-Massin *et al.*, 2012; Guevara *et al.*, 2018). Optimal model selection was based on Akaike's Information Criterion (Akaike, 1974) corrected for small sample sizes (AICc; Hurvich &Tsai, 1989), selecting the most parsimonious model on the candidate set of models showing a ΔAIC<2.

Regarding model performance, we used Continuous Boyce index (CBI; Hirzel *et al.*, 2006) as a threshold-independent metric of how predictions differ from a random distribution of observed presences (Boyce *et al.*, 2002). CBI is consistent with a Spearman correlation (rs) and ranges from −1 to +1. Positive values indicate predictions consistent with observed presences, values close to zero suggest no difference with a random model, and negative values indicate areas with frequent presences having low environmental suitability. We calculated mean CBI using five-fold cross-validation on 20% test data with a moving window for threshold independence and 101 defined bins in the R package enmSdm (Smith, 2019). We further tested the optimal predictions against random expectations using partial Receiver Operating Characteristic ratios (pROC), which estimate model performance by giving precedence to omission errors over commission errors (Peterson, Papes¸, & Soberon, 2008). Partial ROC ratios range from 0 to 2 with 1 indicating a random model. Function parameters were set with a 10% omission error rate, and 1000 bootstrap replicates on 50% test data to determine significant (α ¼ 0:05) pROC values >1.0 in the R package ENMGadgets (Barve & Barve, 2013).

Detail of SPA Tejo Internacional, Erges e Pônsul, which shelters the largest Cinereous Vulture colony in Portugal.©VCF

3. RESULTS

Only one candidate model had an ΔAICc ≤ 2. The best-fit SDM (ΔAICc = 0.0) had a beta coefficient penalty of β = 1 with linear and quadratic terms as model parameters, with high-calibration accuracy (mean CBI = 0.842) and was robust against random expectations (pROC = 1.965, SD = 0.017, range: 1.888–1.991). The optimal model shrinkage penalty was able to retain 13 non-zero beta coefficients, setting to zero the quadratic terms of temperature seasonality, precipitation of wettest month and elevation (Table 2), meaning most covariate terms were highly informative to model prediction (Figures S1-S3 in Appendix).

Table 2. Parameter estimates from the penalised linear and quadratic beta coefficients derived from the response functions for each environmental covariate from the optimal Species Distribution Model for the Cinereous Vulture across the project area.

Covariate	Linear	Quadratic
Temperature seasonality (bio4)	0.027	0
Precipitation of wettest month (bio13)	0.041	0
Eastness	0.136	-0.685
Human Footprint Index	-0.002	NA
NDVI_Dec-to-Feb	0.001	NA
Northness	-0.257	-0.798
Slope	0.317	-0.009
Elevation	NA	0
Small ruminant density	0.141	-0.001
Proportion of open habitat	0.448	NA

From the penalised beta coefficients (Table 2), Cinereous Vultures were most positively associated with two covariates associated to foraging habitat quality at the home range level (inside 40 km buffers around the nests): i.e. proportion of open habitats and small ruminant density. Cinereous Vultures had a quadratic response to the proportion of open habitat with a sharp increase in occurrence between 0 and 25% (Table 2, Fig. 3). Occurrence probabilities hit a plateau and remained at high level (~1) after 25% of open habitat. Occurrence probability reached a maximum around 50 small ruminants/km and decreased at higher density (Fig. 3).

Slope at the breeding site was also strongly and positively associated with the probability of nest occurrence, which increased sharply for slope values between 0 and 15 degrees (Table 1; Fig. 3). Occurrences peaked in locations featuring slopes ranging from 12 to 22 degrees, while declining on steeper slopes, but this may have been because these are rarer in the region sampled. Cinereous Vultures exhibited a unimodal response to both Eastness and Northness, which are related to the orientation of the slope where their nests are located (Fig. 3). This suggests that nest exposure did not affect the breeding occurrence of Cinereous Vultures.

Cinereous Vultures exhibited a positive correlation with temperature seasonality. The relationship between occurrence and bio13 was quadratic with occurrence probabilities peaking in regions experiencing up to 70 mm of precipitation during the wettest month (Table 2). However, probabilities declined sharply in areas with higher precipitation levels (Fig. 3). As expected, Human footprint had a negative effect on Cinerous Vulture occurrences, with predicted values of occurrence falling sharply for HFI values >100 (Table 2, Fig. 3).

Cinereous Vultures had a positive response to NDVI during the pre-laying period (December to February) indicating that the presence of evergreen trees in winter influences the choice of breeding sites for our study species (Table 2, Fig. 3).

Across the study area, our model highlighted four different patches of high habitat suitability for the Cinereous Vulture straddling the border between Portugal and Spain (Fig. 4). From South to North, a first small patch of relatively high habitat suitability was identified in the Serra Algarvia, which includes Special Area of Conservation (SAC)/SPA Caldeirão (PTCON0057) outside of the project study area (Fig. 5). Largest patches of highly suitable habitat were predicted in Spain in Sierra Pelada with discontinuous patches of suitable habitats extending up to the East until Sierra Morena (Fig. 4). Sierra Pelada has already important breeding colonies for this species. Third hotspot of high habitat suitability was predicted from Serra de S. Mamede (including SAC São Mamede, PTCON0007) to the SPA Tejo Internacional, Erges e Pônsul in Portugal, and Sierra de San Pedro in Spain. This patch was connected further North to the highly suitable areas located in SPA Serra da Malcata in Portugal and SPA Sierra de Gata y Vale de Pilas in Extremadura, Spain (Fig. 4). Sierra de San Pedro in Spain is also a well-known stronghold of the species, with hundreds of nests. Finally, the northernmost hotspot of suitable habitat predicted by our model stretched along the border between Spain and Portugal from Puerto Seguro in Spain covering SPA Vale do Côa, SPA Douro Internacional e Vale do Águeda, SPA Rios Sabor e Maçãs, and, within our study area, also until the Eastern part of SPA/SAC Montesinho/Nogueira (PTZPE0003, PTCON0002) (Fig. 5).

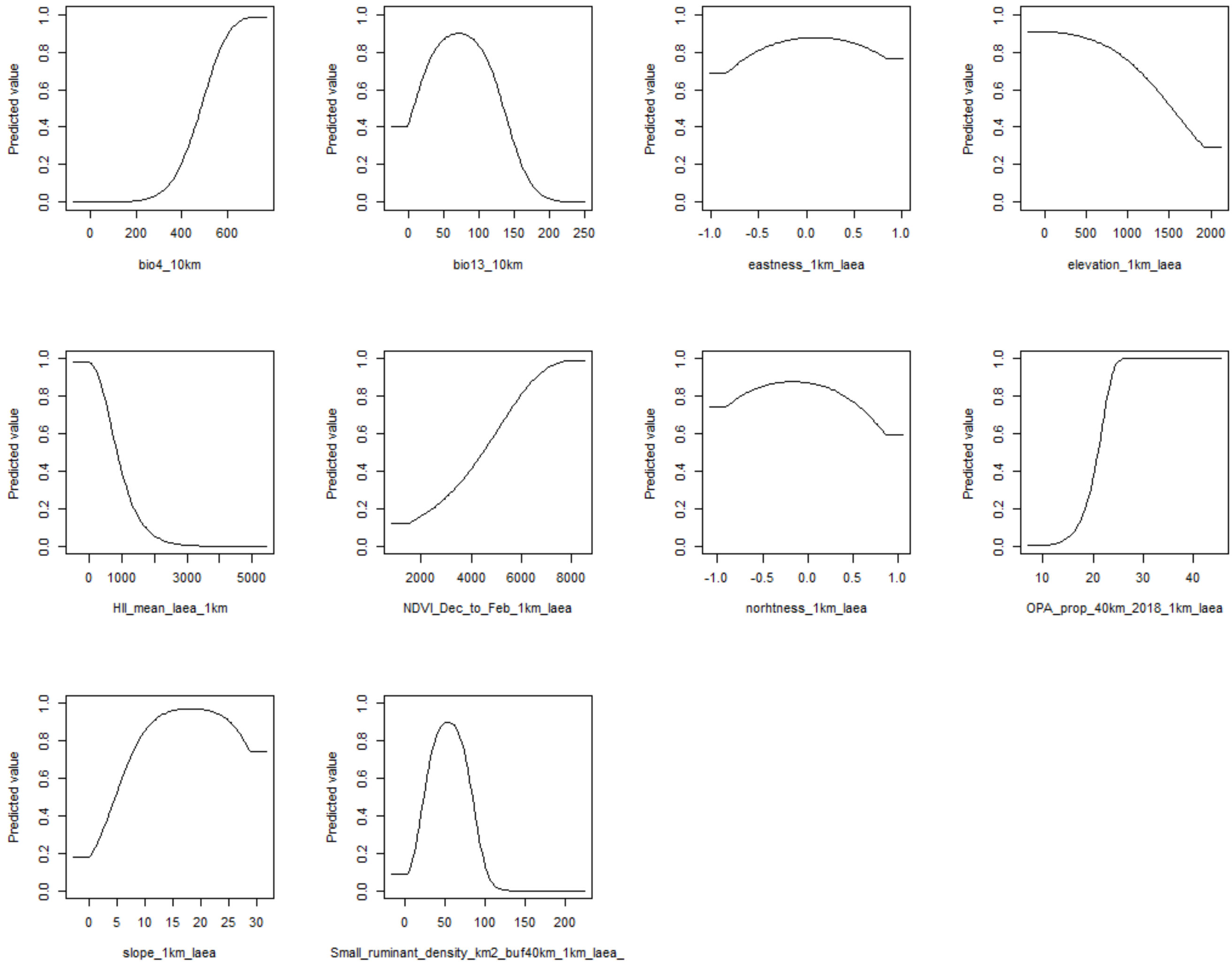

Fig. 3. Penalised logistic regression response functions for each environmental covariate from the optimal Species Distribution Model for the Cinereous Vulture across the study area. The curves show the contribution to model prediction (y-axis) as a function of each continuous habitat covariate (x-axis). Maximum values in each response curve define the highest predicted relative suitability. The response curves reflect the partial dependence on predicted suitability for each covariate and the dependencies produced by interactions between the selected covariate and all other covariates.

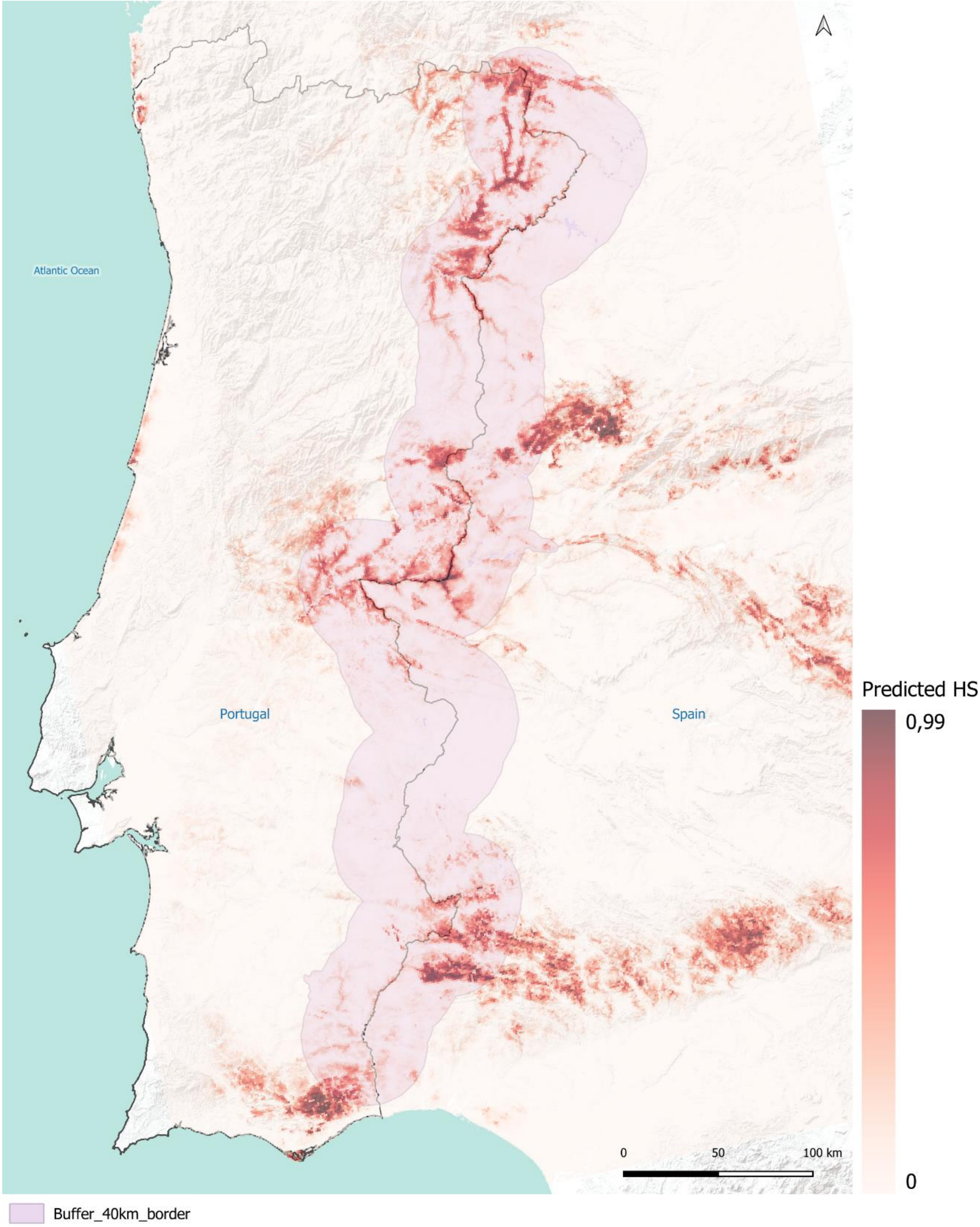

Fig. 4. Continuous species distribution model for the Cinerous Vulture across the study area (Portugal and South-Central western Spain) using a penalised logistic regression model algorithm. Map denotes habitat suitability prediction with dark red areas (values closer to 1) having highest habitat suitability.

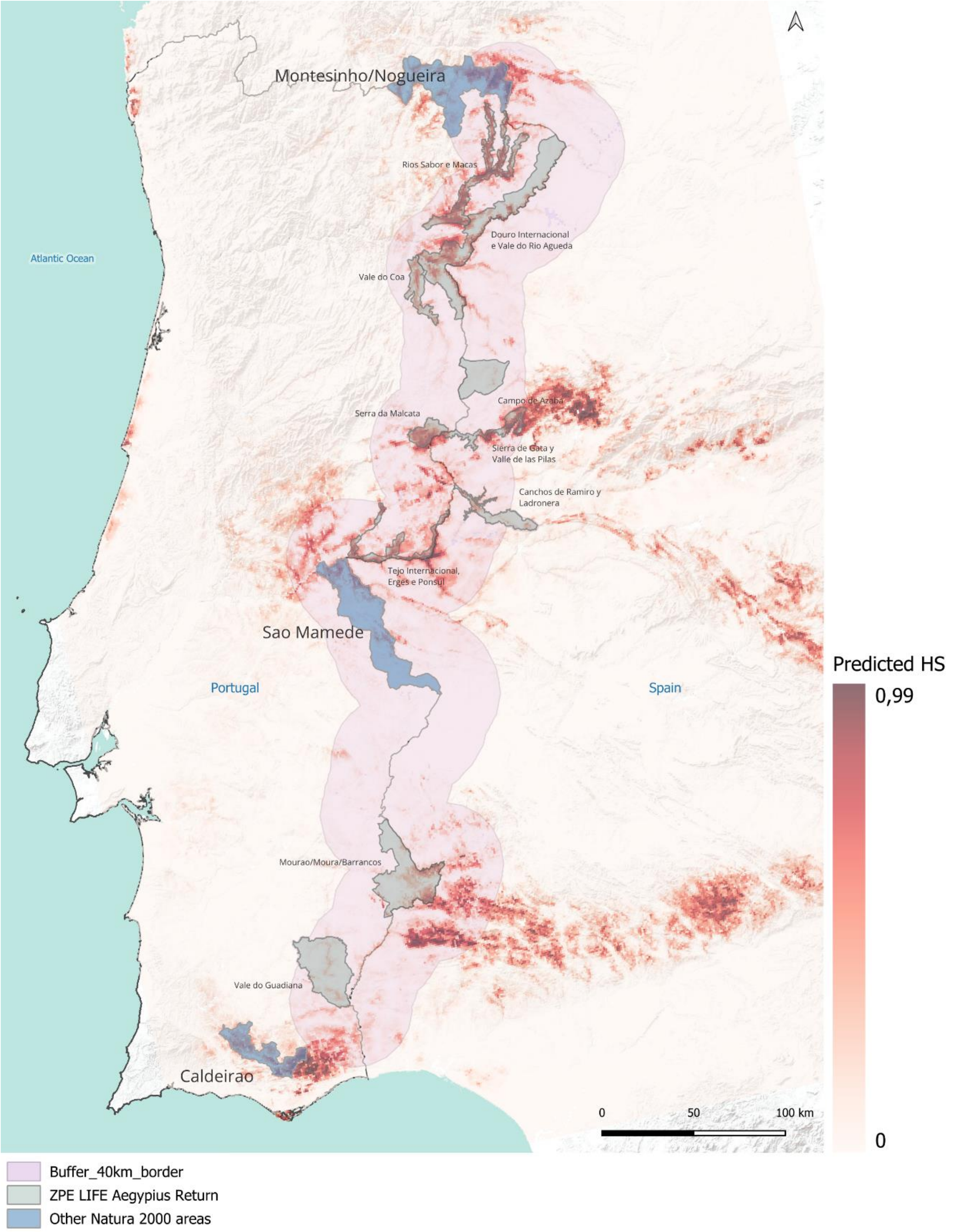

Fig. 5. Continuous species distribution model for the Cinerous Vulture across the study area (Portugal and South-Central western Spain) using a penalised logistic regression model algorithm. Map denotes habitat suitability prediction with dark red areas (values closer to 1) having highest habitat suitability. The LIFE Aegypius Return 10 target SPA and 3 other Natura 2000 areas with high habitat suitability for the Cinereous Vulture, near or within the project's study area, are also shown.

4. DISCUSSION

Our Species Distribution Model has clearly identified hotspots of habitat suitability across the project area in Portugal and Western Spain, but also in the wider area in Iberia. This study provides an initial framework for spatial prioritization of field investigations into potential breeding sites, aimed at monitoring the recolonization of the Cinereous Vulture across the project area. These results will assist stakeholders in selecting candidate monitoring sites or invest in nesting platforms or supplementary feeding areas in currently unoccupied areas where nesting habitat appears most suitable and, hence, recolonization and connectivity can be fostered.

4.1. The Cinereous Vulture's ecological niche in Western Iberia

Our findings highlight the crucial role that environmental factors play, both locally and on a larger scale, in influencing the breeding distribution of Cinereous Vultures. Our results showed that breeding sites were characterized by steep slopes, high NDVI values, and low human footprint. This is consistent with previous studies that have demonstrated that Cinereous Vultures prefer forest patches in rugged areas for breeding, distant from human settlements (Moran-Lopez *et al.* 2006a; Mihoub *et al.* 2014).

Slopes may be advantageous for the construction of nests because of their updraughts. Indeed, air currents facilitate the Cinereous Vulture's take off (Cramp & Simmons, 1980), and the currents are more frequently available on hillsides. Slopes may also provide protection against predation or disturbances (Donázar *et al.*, 2002; Moran-Lopez *et al.*,2006b, Mihoub *et al.* 2014), and provide excellent viewpoints from the nest perspective to detect approaching threats.

Slope orientation can impact breeding habitat selection in raptors, as it affects nest exposure and results in small-scale variations in local microclimatic conditions. Severe conditions at the nest site, including prolonged extreme heat or cold, can impact egg development and the survival of young chicks that are unable to regulate their body temperature. Our results indicated that breeding occurrence was minimal in locations with very low and very high northness values, aligning with previous research that highlights seasonal temperature harshness as a limiting factor at both extremes for Cinereous Vulture nest site selection (Moran-Lopez *et al.* 2006b). However, the relationship between nest site selection and orientation is likely influenced by spatial variations in weather conditions and topography across the study area. For instance, Lima (2006) found that in the Spanish part of Tejo Internacional, Cinereous Vultures preferentially chose sites with a northern exposure. In the Tagus Valley, where summer temperatures are extremely high, Cinereous Vultures likely select sites that maximize shading and reduce the heat experienced by the nestlings.

In addition, Moran-Lopez *et al.* (2006b) showed that, in Extremadura, nest sites of Cinereous Vultures were located further from villages and transport infrastructures (roads and tracks). As other tree-nesting raptors, Cinereous Vultures are particularly sensitive to human disturbance during the breeding season, and human avoidance is probably a key driver of breeding habitat selection in this species (Fargallo *et al.* 1998).

Habitat composition at the site level scale is also important. Cinereous vulture pairs start constructing their nests in winter when deciduous trees do not bear any leaves. Sites with high NDVI values during winter thus indicate evergreen forest patches (cork and holm oaks and coniferous species, such as *Pinus* spp. in central and southern Portugal, or *Juniperus oxycedrus* in the Douro region) that are particularly selected for breeding by the Cinereous Vulture across its distribution range.

Variables related to foraging habitat quality at the home range scale were critical determinants of Cinereous Vulture breeding occurrence. The percentage of open areas and the density of small livestock (sheep and goats) positively influenced breeding occurrence. As central place foragers during the breeding season, Cinereous Vultures require suitable foraging habitats in proximity to their nests (Carrete & Donazar, 2005). The availability of food resources affects Cinereous Vultures' fitness and is a crucial component of habitat quality around the nest site. Our findings align with previous studies (Carrete & Donazar, 2005; Garcia-Baron *et al.*, 2018), which demonstrate that in Spain, the presence of this species is positively associated with scrubland and open areas known as "dehesa/montado"—a habitat type included in the 'open habitat' category of this study (see Materials and Methods). These habitats are frequently used for livestock grazing, support high rabbit and wild ungulate densities, and consequently may provide high food availability and accessibility for Cinereous Vultures.

4.2. Identifying candidate sites for Cinereous Vulture recolonization in the project area

The main hotspots of habitat suitability identified by our Species Distribution Model share obviously some ecological traits, but are generally distinct in terms of biodiversity and landscape composition.

Serra Algarvia, which in its westernmost part includes the SAC/SPA Serra do Caldeirão, is an area of low population density, mainly due to changes in the socioeconomic framework of the region. Since the 1960s, there has been a gradual abandonment of agriculture, namely cereal crops, which resulted in general land abandonment and, consequently, a gradual recovery of the vegetation and soils. The vegetation is mostly scrubland (e.g. *Cistus ladanifer*, *Cistus populifolius*, *Arbutus unedo*, *Erica arborea*) and has some tree cover, mainly cork oak (*Quercus suber*), some deciduous trees, and residually some stone pine (*Pinus pinea*). Agricultural abandonment has led to greater ecological tranquillity, which allowed the establishment of sensitive fauna, such as carnivore mammals (e.g. *Felis silvestris*, *Mustela putorius*) and raptors (e.g. *Aquila fasciata*, *Circaetus gallicus*, *Bubo bubo*). The most suitable areas for Cinereous Vulture identified in this region are located outside the LIFE Aegypius Return's study area and are not protected within Natura 2000, which limits the project's intervention capacity. Also, this region is rarely used by the tagged Cinereous Vultures the partners are monitoring so far. However, this region is only at about 75km from the closest known colony (Sierra Pelada), hence partners will continue to monitor the birds' movements, explore the region as possible during field visits, and disseminate these results to the local authorities and environmental NGO that operate in the region.

The Sierra Pelada and Sierra Morena regions in Spain serve as significant habitats for the Cinereous Vulture, and include already some of the most important colonies for this species.

They are both characterized by mountainous terrain with a mix of Mediterranean forests, scrublands, and rocky outcrops, as well as forestry areas in the case of Sierra Pelada. The area includes extensive dehesa landscapes, which are a traditional type of agroforestry system combining pastureland, trees (usually evergreen oaks), and sometimes croplands.

These sierras have abundant livestock and wildlife that contribute to the food supply for the vultures through natural mortality and big game hunting.

Both regions have areas that are protected within the Natura 2000 network [namely Sierra Pelada y Rivera del Aserrador (ES0000052), Sierra de Aracena y Picos de Aroche (ES0000051), Sierra Norte de Sevilla (ES0000053) and Sierra de Hornachuelos (ES0000050)] or managed to minimize human disturbance, which is crucial for the breeding success of the Cinereous Vulture. Conservation efforts include habitat protection, anti-poisoning campaigns, and supplementary feeding programs.

The overall region falls mostly outside the project area and does not include any of the project's target SPA, which limits its intervention capacity. However, it is very frequently used by tagged Cinereous Vultures and already includes Cinereous Vultures breeding colonies, namely of Sierra Pelada and Sierra Norte (with over 100 breeding pairs each), and of Sierra de Hornachuelos (with over 50 breeding pairs) (Dobado y Arenas, 2018), which means it is an important source of birds potentially recolonising Portugal. The project will therefore enhance the ongoing cooperation with the regional authorities and collaborate in monitoring and conservation activities as much as possible.

Along the entire border strip between the São Mamede and Malcata mountain ranges, passing through the international stretch of the Tagus (*Tejo*) River and its tributaries, most of the territory is protected both by the National and the Natura 2000 Networks of Protected Areas, namely, from south to north:

1. Serra de São Mamede Natural Park;
2. SAC São Mamede;
3. Tejo Internacional Natural Park;
4. SPA Tejo Internacional, Erges e Pônsul;
5. Serra da Malcata Nature Reserve;
6. SAC Malcata (PTCON0004);
7. SPA Serra da Malcata.

This confirms the great importance of this region for nature conservation, particularly for endangered bird species.

In general, these areas have a low population density, with a few urban settings, which reduces human pressure on species and habitats and provides the tranquillity that the Cinereous Vulture, among other species, requires in its breeding areas. São Mamede (1.025m), Penha Garcia (816m) and Malcata (1.078m) encompass higher-altitude areas with steeper slopes, due to the existence of quartzite outcrops (São Mamede and Penha Garcia), or rounder relief but with fairly steep slopes (Malcata). The Tejo Internacional and tributaries areas comprise the respective valleys with river scarps and sloping hillsides at lower altitudes (between 120m near the Tejo and 386m in Salvaterra do Extremo).

Regarding trees coverage, the whole region is covered by evergreen species, and many large trees which the Cinereous Vultures select to built their nests on. The mountain ranges have woods or isolated maritime pines (Pinus pinaster), as well as cork and/or holm oaks patches with a well-developed shrub layer.

Due to the soil and climate conditions and the cereal exploitation that took place until the 1960s, which led to soil degradation, the Tejo Internacional vegetation is dominated by patches of holm oak (*Quercus rotundifolia*), sometimes with some cork oak (*Quercus suber*), mixed with very diverse Mediterranean scrub species, such as *Cistus* spp., rosemary (*Lavandula* spp.), strawberry tree (*Arbutus unedo*), lentiscus (*Phillyrea angustifolia*), mock privet (*Phillyrea latifolia*), Italian buckthorn (*Rhamnus alaternus*), mastic tree (*Pistacia lentiscus*), terebinth (*Pistacia terebinthus*), among others.

In the whole area, extensive livestock (mostly small ruminants and bovines) and hunting [red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*), wild boar (*Sus scofa*) and European mouflon (*Ovis orientalis musimon*)] estates are very common and represent abundant food sources for the Cinereous Vulture and other scavenging species.

As the Cinereous Vulture is a philopatric species, the existence of stable breeding colonies in close Spanish territories favours the species' expansion and consolidation in Portugal. The Tejo Internacional breeding colony, which was only reestablished in 2010, has breeding pairs in both sides of the border, only a few hundred meters apart. Other breeding territories (e.g. Sierra de San Pedro, Canchos de Ramiro and Sierra de Gata) are only a few kilometers away (12km from Serra de São Mamede Natural Park; 20km from Serra da Malcata Nature Reserve). Although the project's intervention capacity is limited outside the target SPAs, transboundary and intersectoral cooperation will be key to continue to adequately monitor the Cinereous Vulture's populations in this area, paying special attention to potential new settlements, and assure quality breeding habitat and connectivity through the reduction of threats (such as forest fires, poisoning, and powerline related mortality), and the reinforcement of food availability.

Northeastern Portugal features several interconnected SPA and SAC, including Douro Internacional, Rios Sabor e Maçãs, and Vale do Côa, all part of the target project's Natura 2000 areas, and also Montesinho/Nogueira. Such areas frequently overlap with the Portuguese Network of Protected Areas. These regions are characterized by a low population density and rural settings where traditional agricultural lifestyles prevail. Small-scale agriculture, forestry, and eco-tourism shape the socioeconomic framework, with communities engaged in subsistence farming, livestock rearing, and sustainable practices influenced by the natural landscape and conservation efforts.

The Douro Internacional e Vale do Águeda SPA includes Mediterranean forests, scrublands, and riparian habitats, with key species such as oaks, cork oak, junipers and various shrubs. Agriculture, forestry, and conservation areas coexist, with vineyards and olive groves on the lower slopes and grazing and natural habitats higher up.

Montesinho/Nogueira features extensive forests including Pyrenean oak, chestnut, and maritime pine, alongside meadows, wetlands, traditional agriculture and pastures.

Rios Sabor e Maçãs is an important North-South ecological corridor which connects all these areas and encompasses riparian habitats with willows (*Salix* spp.), alders (*Alnus glutinosa*), and other moisture-loving plants, as well as upland dry grasslands and Mediterranean-type shrublands. Here, agriculture is well balanced with river habitat conservation.

Vale do Côa includes agriculture, particularly olives and almonds, grazing, natural scrubland, and cultural heritage conservation integrated with tourism.

Mammals common to these regions include the Iberian wolf (*Canis lupus signatus*), wild boar (*Sus scrofa*), and roe deer (*Capreolus capreolus*), with Montesinho/Nogueira also supporting red deer (*Cervus elaphus*) populations.

These SPA are vital for bird conservation, hosting species such as the golden eagle (*Aquila chrysaetos*), Bonelli's eagle (*Aquila fasciata*), and all the vultures that breed in Portugal: the Egyptian (*Neophron percnopterus*), the Cinereous, and the Griffon (*Gyps fulvus*) vultures. This Cinereous Vulture colony is the smallest, the most fragile and isolated in Portugal, being over 100km from the closest breeding area in Spain, and has increased from three to seven breeding pairs in 2024. It this hence particularly important to monitor the colony and surrounding areas for possible new colonizations.

The SPAs form a network of habitats supporting diverse species and ecological processes, while also contributing to local communities. Collaborative management involving local communities, governmental agencies, and conservation organizations ensures the effectiveness of conservation actions, as is planned within LIFE Aegypius Return in what concerns habitat management, fire prevention, antipoisoning campaigns, and support to extensive livestock management and farming. In this region, the cooperation is also transboundary in what directly implies the Cinereous Vultures monitoring and conservation.

4.3. Conservation implications within the framework of the LIFE Aegypius Return project

The habitat suitability map identified four primary patches of areas suitable for nesting along the Spain-Portugal border within the project area, and further afield, located in the northern, central, and southern regions. Currently, the availability of nesting sites does not appear to be a limiting factor for this population.

The identified habitat suitability hotspots will help direct the next phases of the project. Partners will closely monitor the tagged cinereous vultures, paying additional attention to the habitat use in the highlighted areas, and intensify field prospection in potential nesting sites that could be colonized. Potential threats at these sites, such as energy infrastructure (Vasilakis *et al.* 2016), will also be identified and mitigated.

Conservation actions should address the species' requirements at various spatial scales. Potential nesting sites, characterized by well-oriented hill slopes with evergreen trees, should be protected from human disturbance, especially during the laying and incubation periods. Recent studies have highlighted the increasing practice of outdoor recreational activities in European mountains as a potential threat to sensitive wildlife species (Tobajas *et al.*, 2022). Therefore, controlling these activities in suitable and occupied nesting habitats should be a priority. Additionally, monitoring human disturbance in suitable but currently unoccupied areas is essential to enhance the likelihood of recolonization by the study species.

Land abandonment in Mediterranean mountain areas has significantly impacted landscape structure, leading to cascading effects on biodiversity (Garcia-Baron *et al.*, 2018). Our results emphasize that maintaining traditional agroecosystems is crucial for the conservation and restoration of the Cinereous Vulture in Portugal and Western Spain. Maintaining or restoring high-quality foraging habitats and food resource availability around potential breeding territories is key to consolidating and expanding the Cinereous Vulture population in Portugal. Previous research has shown that Portuguese policies on livestock carcass disposal may reduce vulture foraging opportunities across the project area (Arrondo *et al.* 2018). Therefore, measures aimed at supporting extensive pastoralism practices should be paired with the implementation of livestock carcass disposal solutions which result in larger food availability for vultures, such as traditional supplementary feeding sites, but also *unfenced feeding areas* within the extensive livestock estates, as proposed by the LIFE Aegypius Return project under the EC Regulation 1069/2009, and the Portuguese legislative Dispatch no. 3844/2017, which still needs to be widely implemented.

4.4. Study limitations

A frequently mentioned limitation of Species Distribution Models in scientific literature is that the ecological niche based on current habitats occupied by threatened species does not accurately reflect the historical ecological niche these species may have occupied (Montsarrat *et al.* 2019). The distribution of apex predators and scavengers, like the Cinereous Vulture, has been significantly affected by centuries of human persecution and disturbance. Consequently, the habitats currently occupied by many species often serve as refuges, representing only a fraction of their original ecological niche (Kerley *et al.* 2020). With effective conservation measures, large predators and scavengers are recolonizing areas of their original distribution, including habitats previously considered unfavorable (Martinez-Abrain *et al.* 2019). Consequently, SDMs based on the current ecological niche of these species may fail to identify habitat patches that are being recolonized or are likely to be recolonized in the near future. For example, in late spring 2024, a new breeding pair of Cinereous Vultures was discovered in Southern Portugal, outside the study area and at about 55km from the closest breeding colonies (either Herdade da Contenda in Portugal or Sierra Pelada in Spain), in a patch not highlighted by our model presented here.

In addition, our results showed no relationship between Cinereous Vulture breeding occurrence and the two nest exposure variables, Eastness and Northness. To extract the exposure variables, we resampled the original 100m resolution elevation raster layer to 1km to homogenize the spatial scale used for all environmental variables at the local scale. This decision may have obscured the relationship between Cinereous Vulture habitat selection patterns and fine-scale variations in nest exposure. While this resampling is unlikely to affect the large-scale habitat suitability outcomes of this SDM, future analyses could use exposure variables extracted at a finer scale (e.g., 250m) to determine if the relationship between exposure variables and breeding occurrence becomes clearer.

5. CONCLUSIONS

Utilizing nest occurrence data from extensive monitoring programs conducted by the project partners and nature conservation national authorities from Portugal and Spain, we employed advanced spatial modelling tools to predict habitat suitability for the Cinereous Vulture across the LIFE Aegypius Return project area. These results will inform monitoring efforts and conservation planning within the LIFE project framework, focusing on areas identified as highly suitable. This includes ground-truth validation of the Species Distribution Model results and the implementation of conservation actions, such as mitigating anthropogenic threats and managing habitat and food resources. These measures aim to facilitate the recovery of the Cinereous Vulture population in Portugal by promoting the expansion of its breeding population into currently unoccupied but highly suitable areas.

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Adult and chick Cinereous Vulture in the nest – breeding colony at Herdade da Contenda, southern Portugal. Shot taken from a long distance to avoid disturbance. ©Eduardo Santos/LPN

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8. APPENDIX

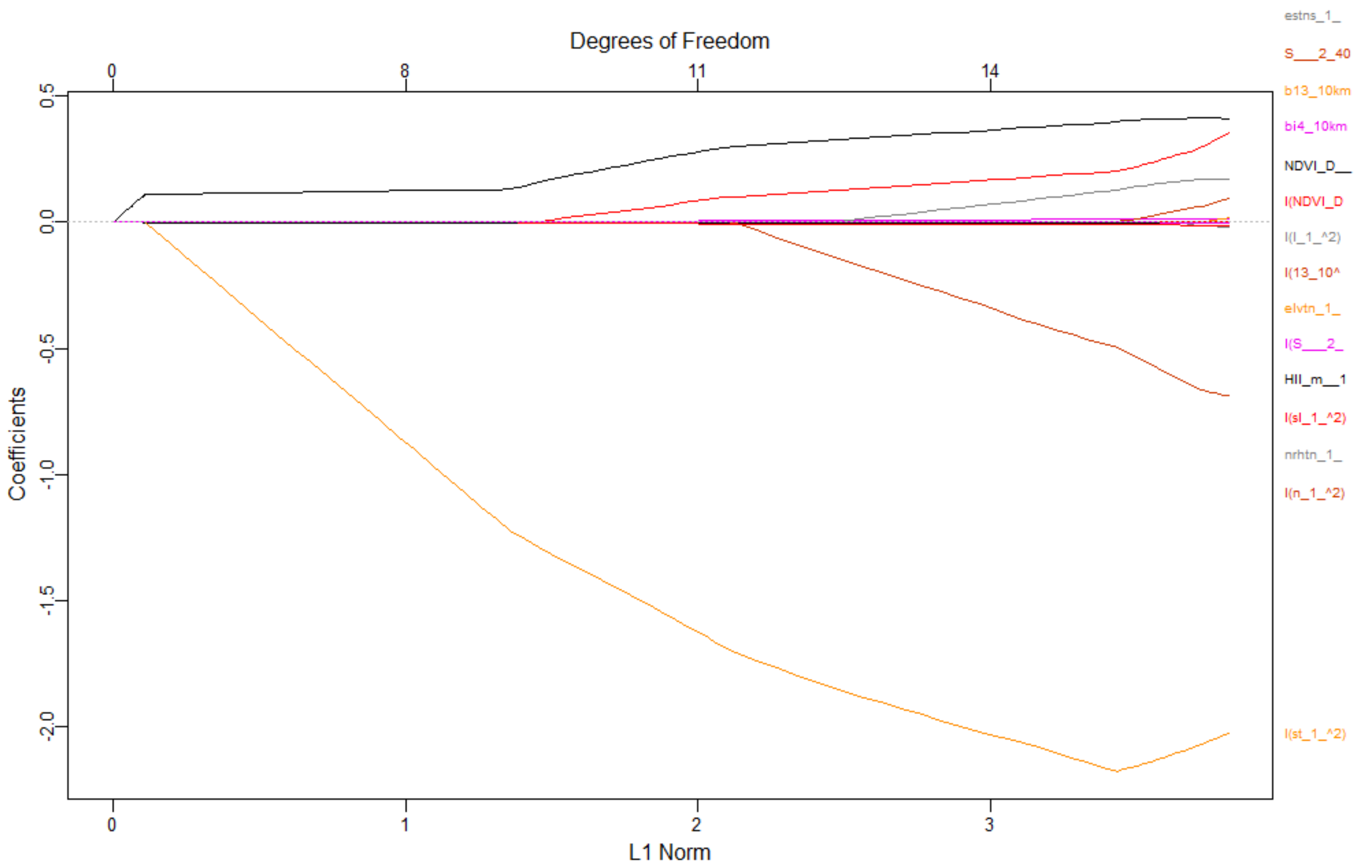

Figure S1. Beta coefficient paths for the optimal penalized logistic regression model where each curve corresponds to a covariate term (linear and quadratic). The paths of each coefficient term are plotted against the fraction deviance explained on the training data. The upper axis indicates the number of non-zero coefficients at the current lambda which is the effective degrees of freedom for the elastic net.

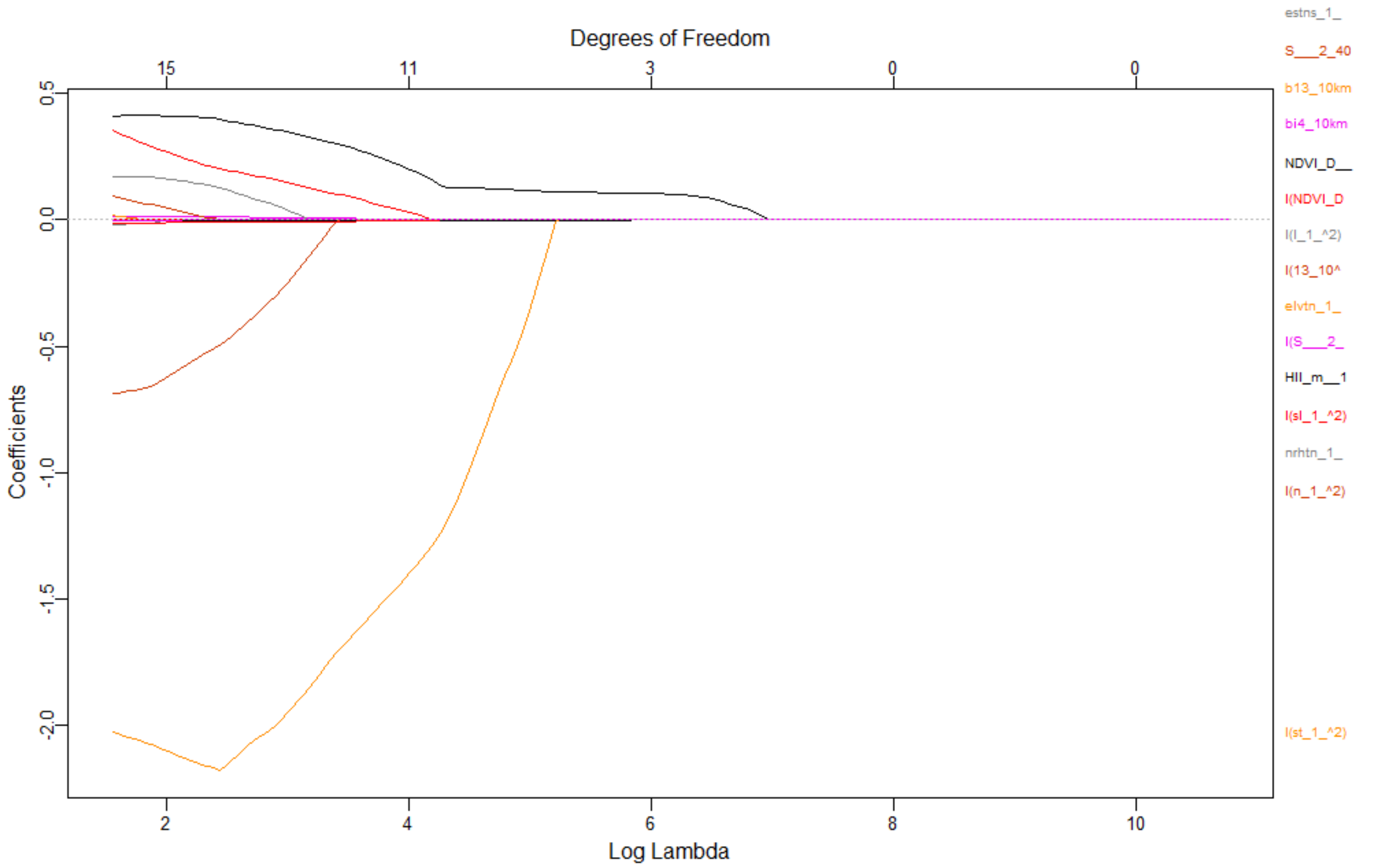

Figure S2: Beta coefficient paths for the optimal penalized logistic regression model where each curve corresponds to a covariate term (linear and quadratic). The paths of each coefficient term are plotted against the L1-norm (lasso or elastic net) of the whole coefficient vector as lambda (the amount defining the level of coefficient shrinkage) varies. The upper axis indicates the number of non-zero coefficients at the current lambda which is the effective degrees of freedom for the lasso or elastic net.

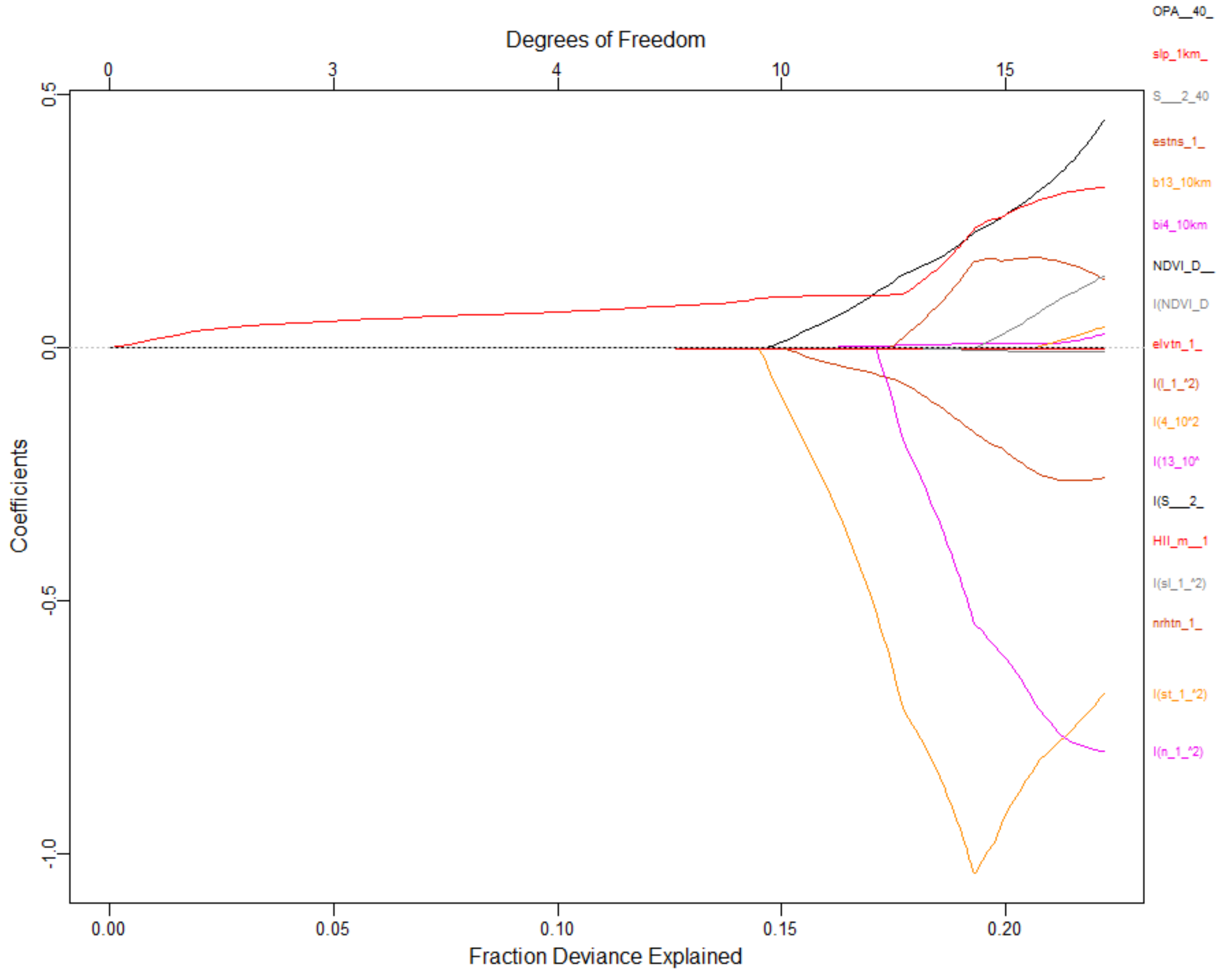

Figure S3: Beta coefficient paths for the optimal penalized logistic regression model where each curve corresponds to a covariate term (linear and quadratic). The paths of each coefficient term are plotted against the log-lambda of the whole coefficient vector as lambda (the amount defining the level of coefficient shrinkage) varies. Log-lambda on the y-axis indicates the log of the optimal value of lambda which minimizes the prediction error. This lambda value will give the most accurate model. The upper axis indicates the number of decreasing non-zero coefficients at the current lambda which is the effective degrees of freedom for the elastic net.