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RESEARCH

Mapping wild boar density across Europe: combining spatial models and density estimates

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Abstract
The wild boar population in Europe has been growing in recent decades prior to the arrival of African swine fever (ASF), which has now spread across much of eastern Europe. We obtained two independent sources of wild boar data: occurrence sightings and hunting harvest. We combined these with environmental predictors and used them in two species distribution modelling approaches, a Maxent approach for occurrence data and a GLMM for the hunting harvest, to produce output at the European level. The output of these models was then combined with robust and comparable density estimates from 77 sites across Europe to produce a density estimate and total population size for each country prior to documenting ASF in that country (from 2007 for Georgia to 2022 for most EU countries that are still free from disease). The output indicates a total population of wild boar in Europe between 13.5 and 19.6 million individuals prior to the hunting season each year in the core wild boar range. Population estimates of wild boar in Europe based on occurrence sightings and hunting harvest are highly similar yet vary substantially among countries. Although the output may need to be adjusted where local factors affect the population (e.g., areas of range spread) the output can be used for assessing risk of disease spread and effect of management. We propose that the availability of density estimates from the European Observatory of Wildlife will permit robust population estimates for other species of interest since the methodology is consistent between species and habitats.

Keywords Hunting harvest · Population density · Species distribution model · *Sus scrofa*

Introduction

The population of wild boar (*Sus scrofa*) in Europe has been steadily increasing in recent decades, even as hunting pressure has remained stable or declined (Gaspar et al. 2025; Massei et al. 2015). However, this trend is based on hunting data that are not consistently collected across Europe, making it difficult to accurately assess population dynamics and density (More et al. 2018).

One major consequence of rising wild boar densities is the heightened risk of disease outbreaks. After the introduction in Georgia in 2007, African swine fever (ASF) was first detected in the European Union in 2014 in Lithuania, Poland, Latvia and Estonia (EFSA 2015) and has since spread both locally and through human-related activities (EFSA et al. 2020). ASF has a very high mortality rate in wild boar and domestic pigs. While some success has been achieved in controlling long-distance spread through strong management strategies, including culling, fencing and carcass removal (European Commission 2019; Licoppe et al. 2023; Smith et al. 2022), ASF continues to expand throughout Europe, significantly reducing local populations of both wild boar and domestic pigs (Sauter-Louis et al. 2021).

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Wildlife management across Europe is fragmented, with ASF control strategies varying among countries (Vicente et al. 2019). These differences (e.g. changes in hunting licensing and restrictions on hunting) also influence hunting pressure in unpredictable ways, making it difficult to use hunting records to infer wild boar density after ASF has emerged.

To understand the impact of ASF on wild boar populations and management actions aimed at controlling the disease, it is essential to obtain accurate estimates of population density before disease arrival and to continue monitoring afterward. Density estimates are more informative than relative abundance indices because they provide absolute figures needed for effective disease surveillance, risk assessment, and population management. They also help address conflicts involving wild boar and humans and assess the ecological carrying capacity of habitats. Unlike relative indices, density values are directly comparable across regions and time.

Reliable methods exist for estimating wild boar density at local scales (ENETwild consortium et al. 2018b). At a broader scale, high-quality hunting statistics, when collected at fine spatial resolution, can be used to model long-term trends in relative abundance across Europe (ENETWILD-consortium et al. 2022c; ENETwild consortium et al. 2019). To improve these models, it is necessary to compile and validate wild boar occurrence and abundance data and calibrate them using accurate local density estimates.

In this study, we combined two updated spatial modelling approaches (one based on occurrence data and the other on hunting data) with density estimates from across Europe (ENETWILD-consortium et al. 2022b, 2023). Using predictions at a 2 × 2 km resolution from the European Observatory of Wildlife (EOW) platform (ENETWILD-consortium et al. 2022a: https://wildlifeobservatory.org/) and recent literature (from 2015 onward), we calibrated these models to produce density maps for wild boar in Europe. We then estimated the total wild boar population size by country and evaluated the results.

Methods

To focus on wild boar distribution before the introduction of ASF, we separated sightings into pre- and post-ASF periods. ASF outbreak data were sourced from WAHIS/WOAH, which provided the date and location of confirmed cases in wild boar. The earliest outbreak date in each region (based on GADM, Global Administrative Database, level 1 boundaries) was used to classify sightings accordingly (see Fig. 1). Each area was assumed to be ASF-free in all years prior to detection.

Density data

Wild boar density data were collected from 83 different locations, primarily in late summer or early autumn using the Random Encounter Model (REM) approach (Rowcliffe et al. 2008), as detailed in Table S2. Eleven additional data points were sourced from published literature. We only included data from areas where African swine fever (ASF) had not been detected in wild boar at the time of density estimation, based on the latest updates from the EU ASF Zoning measures (DG Health and Food Safety; see Fig. 1). To ensure data quality and consistency, we applied the following selection criteria: (1) methodological reliability – only studies that followed the field and analytical protocols recommended by the ENETWILD consortium (ENETwild consortium et al. 2018b) were included; (2) estimate uncertainty – each density estimate had to include a measure of uncertainty, specifically the coefficient of variation; (3) georeferenced data – the exact location of each study area had to be clearly georeferenced. The resulting density estimates ranged from 0.18 to 74 wild boar per square kilometre. The highest densities were typically found in protected or periurban areas, where population control is limited and food availability is higher.

Occurrence model

Sightings of terrestrial mammals, including wild boar, were obtained from the Global Biodiversity Information Facility (GBIF) on December 8, 2023 (https://doi.org/10.15468/dl.au5w7a). The data were filtered to include only: human observations with a coordinate uncertainty of 2 km or less (to match a 2 × 2 km ETRS grid cell); unique records (duplicates with the same date, location, and species were removed); sightings recorded after 1985; and observations within the terrestrial landmass of Europe.

Consideration for variable survey effort and species range limitations are important for distribution modelling (Croft et al. 2025b). Survey effort was estimated using sightings of other medium-to-large terrestrial mammals, serving as a proxy for observer activity (Coomber et al. 2021; Croft and Smith 2019; Phillips and Dudík 2008) and stable species range (Fig. 2) was defined using data from the IUCN Red list (IUCN 2021) and Map of Life (Burgin et al. 2020; Mammal Diversity Database 2020; Wilson et al. 2009–2019).

Environmental variables used in the model included climate, land cover/use, topography, and human influence (see Table S1). To reduce multicollinearity, a Variance Inflation Factor (VIF) analysis was conducted, removing variables with VIF scores above 2 (Naimi et al. 2014).

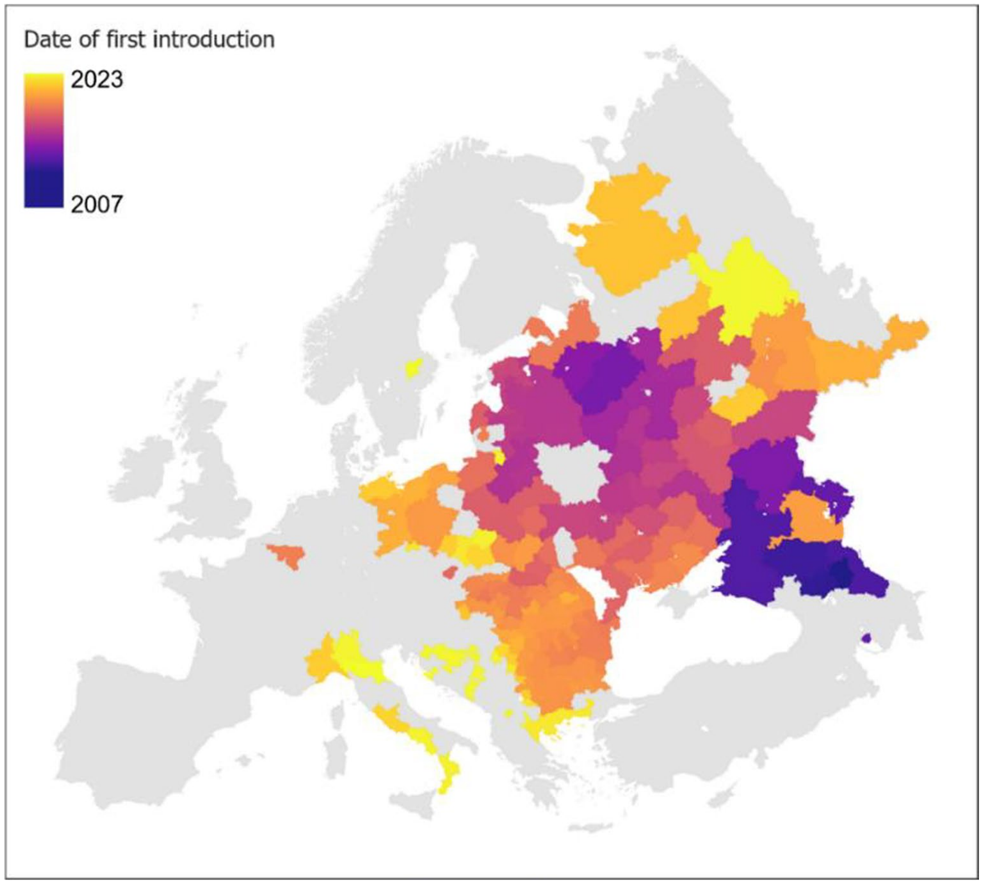


Fig. 1 Map showing date of the first African swine fever outbreaks in wild boar across GADM level 1 administrative boundaries. Darker colours denote earlier dates of African swine fever detected in wild boar

We used Maxent (Phillips et al. 2004), a presence-background modelling approach, to estimate habitat suitability. Since Maxent does not consider non-detections as absences, it only provides a relative measure of habitat suitability rather than a probability of occurrence. However, this is sufficient for our goal of estimating relative abundance. Alternative approaches were considered (e.g. Croft et al. 2025b; Valavi et al. 2021) against the available data (patchy survey effort) and requirements of the study (projection at European extent) and discounted primarily due to the complexity in handling various spatial and temporal biases within the data (Steen et al. 2021). To reduce spatial bias caused by clustered observations (spatial autocorrelation), we applied spatial thinning. This involved randomly subsampling occurrence points to ensure a minimum distance between them and systematically increasing the thinning distance until the model's training AUC (Area Under the Curve) peaked, indicating the best balance between reducing bias and retaining information (Fig. 3). A thinning distance of approximately 60 km was found optimal, aligning with known wild boar dispersal distances (Santini et al. 2013) and a deterministic thinning method, geoThin (Smith et al. 2023), was used to generate a single, reproducible model.

Using the model output and reliable wild boar density estimates from the EOW (Table S2), we created a Pan-European density map as follows. For the determination of reliable density estimates of multiple species, considering all the pros and cons of the available methods (ENETwild consortium et al. 2021), camera trapping was selected as a non-invasive and widely applicable and affordable method to collect robust population data. Based on preliminary tests carried out in Iberia (Palencia et al. 2022), the EOW opted for the implementation of standardized Random Encounter Model (REM) approach (Rowcliffe et al. 2008). This model uses the 'ideal gas theory' applied to animals (i.e., animals treated as gas molecules) to estimate population density based on the contact rate (i.e., number of encounters per time unit), animal speed and intrinsic measurements of the detection field of the camera. The formula to estimate the density with REM is:

$$D = \frac{y}{t} \frac{\pi}{vr\,(2+\theta)}$$

where y is the number of encounters, t is the total survey effort, v is the daily range (i.e., product of animal's activity and speed), r is the effective detection radius, and θ is the effective detection angle. Several papers have confirmed the wide applicability

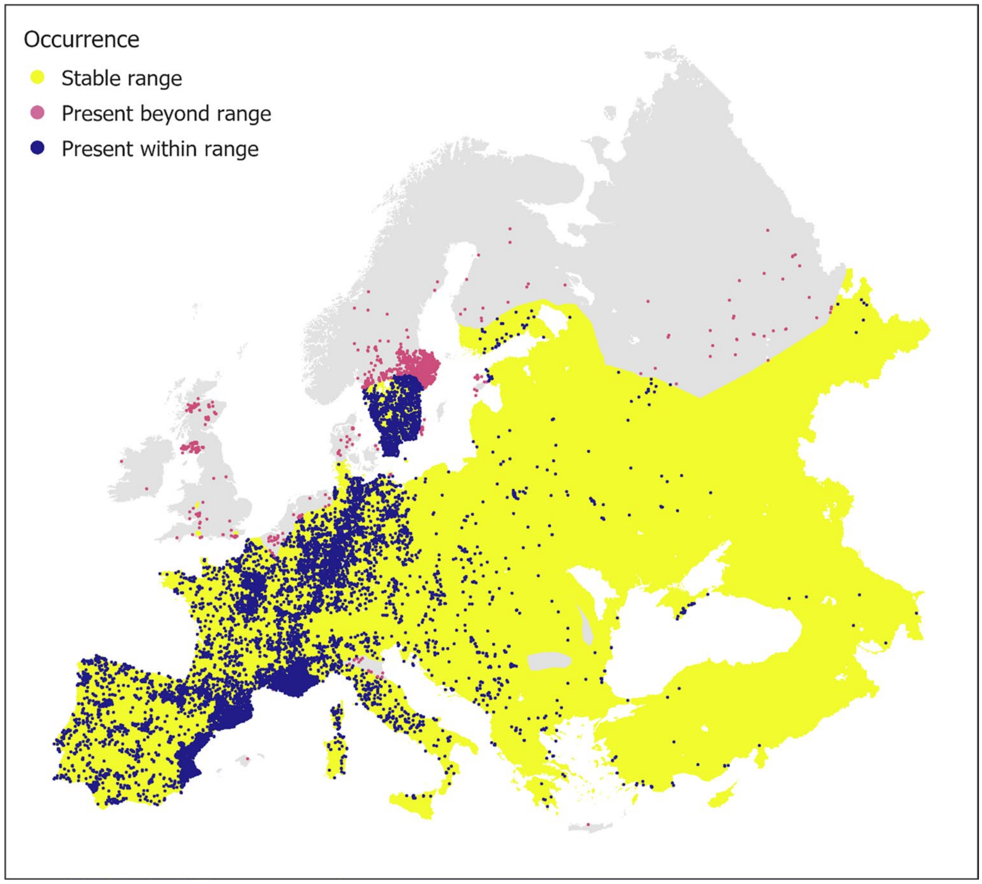


Fig. 2 Map showing Global Biodiversity Information Facility (GBIF) presences and the expert-defined "stable" range for wild boar across Europe

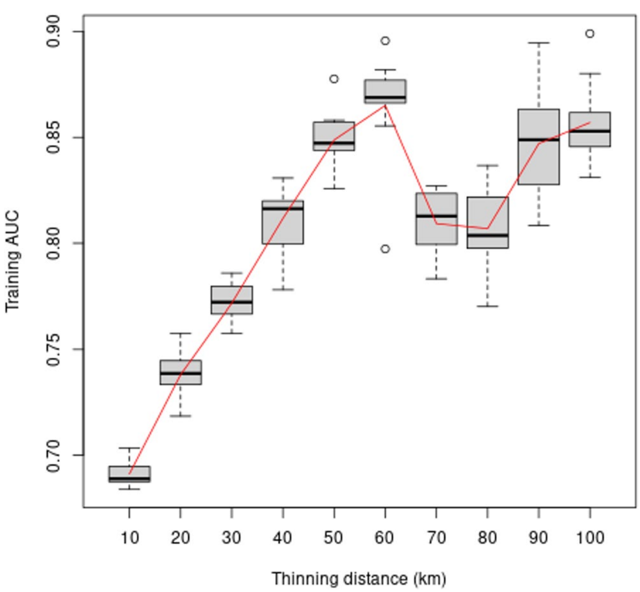


Fig. 3 Box and Whisker plot showing model performance measured using training AUC (Area Under the Curve) based on subsampling of data locations to ensure an increasing minimum spacing of records. The boxes are 25th and 75th percentiles, the main line is the median, and the whiskers are effective minimum and maximum. Optimal minimum spacing appears to occur around 60 km which matches the maximum dispersal distance for wild boar

and reliability of this method with different mammal taxa (e.g. Guerrasio et al. 2022; Jensen et al. 2022; Palencia et al. 2022; Palencia et al. 2021). Regarding the eleven additional data points sourced from published literature, they were included because they applied methods and protocols consistent with recommendations provided by *ENETWILD* guidance on wild boar density estimation (ENETwild consortium et al. 2021).

Each study site with a known density was assigned a boundary polygon corresponding to a local management unit (cameras were distributed across it at regular distances, normally ranging between 1 and 2 km), which were rasterised at a 1 × 1 km resolution. Habitat suitability values from the model were extracted for each raster cell with a known density. A generalised linear model (GLM) was then fitted with wild boar density as the response variable and habitat suitability as the predictor, using a gamma distribution and identity-link function due to the right-skewed nature of the density data. The model was applied across Europe to predict wild boar densities. Finally, the density map was clipped by country boundaries to calculate mean density, and total population estimates per country. The transferability of both models were assessed by producing a Multivariate Environmental Similarity Surface (MESS), which highlights the differences between the environmental space occupied by model training and model projection data (Elith et al. 2010).

Hunting model

To calibrate the hunting yield-based model into wild boar population densities, we first predicted hunting yield (HY) at a 10 × 10 km resolution, following the methodology developed by the (ENETWILD-consortium et al. 2022c). Since 2018, the *ENETWILD* consortium has developed a harmonised, Europe-wide modelling framework that uses hunting harvest data as a proxy for wild boar relative abundance to estimate their spatial distribution and density across Europe, leveraging the most widely available and long-term data source for this species. Spatially explicit statistical models relate hunting yields to environmental and land-use variables while accounting for overdispersion, and spatial autocorrelation, enabling smooth, continuous predictions across borders.

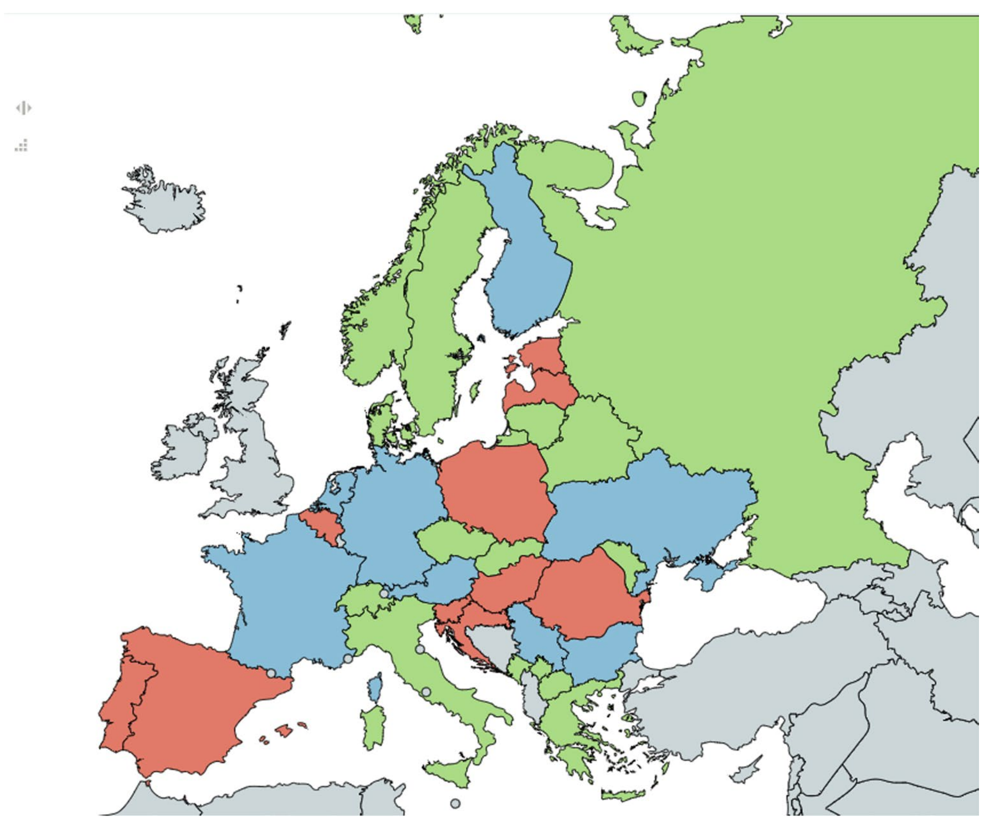
The response variable used in the model was HY density (Fig. 4), defined as the maximum number of individuals harvested annually between the 2015 and 2020 hunting seasons, divided by the area in square kilometres.

We applied the ENETWILD framework for wild ungulates (ENETWILD-consortium et al. 2021, 2022c), using a generalised linear model (GLM) with a negative binomial distribution and a logarithmic link function to identify the most relevant eco-geographical predictors of HY (Cameron and Trivedi 2013). To avoid multicollinearity, we assessed predictor variables using the Variance Inflation Factor (VIF) and excluded any with a VIF above 2. The model was trained on 80% of the data, with the remaining 20% used for validation, i.e., after the model was trained, predictions were generated for this unseen data and compared with the observed values. Final model selection was based on a forward-backward stepwise procedure based on the Akaike Information Criterion (AIC) (Akaike 1974).

To evaluate model performance, we created calibration plots by comparing the mean observed HY within percentile-based intervals of predicted HY from the validation dataset. Ideally, these values should align along the identity line, indicating accurate predictions (Pearce and Ferrier 2001). We also assessed model performance separately across four European bioregions (environmental bioregions as shown in Table S2 and previously used ENETwild consortium et al. 2019), and tested calibration both with and without zero-density values.

From the wild boar density dataset, we used the 77 ASF-free sites. For each site, we extracted the median predicted density of hunted animals within buffer zones of 5, 10, and 15 km. We then modelled density at each spatial scale using a generalised linear mixed model (GLMM). In these models, the response variable was the log-transformed density, while the fixed effects included the log-transformed area of the sampling location (in hectares) and the log-transformed hunting yield. Bioregion was included as a random effect. We compared models across the three spatial resolutions

Fig. 4 Resolution of latest data supplied for wild boar hunting statistics at national level (at least partially within country) used to predict hunting yields at 2 × 2 km: red – hunting ground level data; green – municipality level data; blue- NUTS2 or NUTS3 level data (Nomenclature des Unités Territoriales Statistiques); grey – no data



using AIC to identify the most parsimonious model. This best-fitting model was then used to convert hunting yield data into wild boar population density estimates by downscaling it to a 2 × 2 km resolution across Europe.

Results

Occurrence model

A single habitat suitability model was produced (Fig. 5), and its performance was evaluated by analysing the contribution of different environmental variables. The results showed that factors such as growing season length, precipitation during the warmest quarter of the year, moderate broad-leafed tree cover, herbaceous vegetation, and cropland together accounted for almost half of the model's predictive power (Table S3). The MESS analysis revealed small regions at the extreme edges of our modelled extent (northwestern Scotland, western Norway and southern Türkiye) where environmental conditions were not well represented in the training data, indicating where the model's predictions may be unreliable. The final Maxent model achieved a training AUC score of 0.89, suggesting strong predictive performance. Finally, the suitability scores were converted into absolute density estimates to support further analysis (Fig. 6).

Hunting model

The hunting yield model output (individuals hunted per km^2) for wild boar at 10 × 10 km (Fig. 7) indicates that, among all of continental Europe, relatively few areas are beyond the environmental domain according to MESS analyses. The overall European pattern of wild boar indicates that this species is widely distributed, with very limited presence only in the far north of Scandinavia and some high-altitude or climatically harsh areas. The model highlights a clear south–north and west–east gradient, with generally higher abundance in southern, western, and central Europe compared to northern and northeastern regions. High-abundance regions (> 2.5–10 + hunted boar/km^2) are mainly in the Iberian Peninsula and the Western Balkans, with some of the highest values in Europe, especially in Mediterranean and mixed forest–agricultural landscapes. The regions with moderate-abundance (1–2.5 hunted boar/km^2) occupies much of Central and Eastern Europe, including Poland, Romania, Bulgaria, and the Baltic States. These areas sustain stable to high populations, but generally lower than Mediterranean and Atlantic regions. Low-abundance regions (≤ 1 hunted boar/km^2) includes northern Europe (Scandinavia): wild boar presence is largely restricted to southern Sweden. Eastern Europe and Russia present large areas with low values. Mountainous regions (Alps, Carpathians, Pyrenees) present patchy distribution with lower yields due to altitude and habitat limitations.

The calibration plots for wild boar (Fig. 8) demonstrated strong predictive performance across all bioregions, indicating that the model effectively captures the spatial distribution patterns. Removing zero values from the validation datasets had little impact on the results; in fact, the model's performance slightly improved without them, while still maintaining good predictive accuracy in all regions. A clear density gradient was observed across the continent, with medium to high densities concentrated in Western, and Southern Europe. In contrast, densities declined toward the north and east, with a more scattered pattern of medium to low densities.

The model also predicted moderate to high densities in southern Sweden and Norway, likely influenced by the similarity in climatic conditions to those in the Western bioregion, which may have shaped the model's projections in these areas.

Calibration of predictive models into densities

The results of the model at three spatial scales indicated that a 15 km buffer was the best option (Table 1) as this had the lowest AIC score, so the parameters for this model were determined (Table 2). These parameters confirmed the positive association between local densities and hunting yields, while controlling by effect of the size of the area of the sampling location.

The modelled wild boar density estimation was obtained by fitting the surface of the study area to the median value in the dataset (3,602 ha) and results calculated at a 2 × 2 km resolution (Fig. 9).

Comparison of the two approaches

These two independent approaches of occurrence sightings and hunting yield were then compared at a country level for mean density and calculated total population size (Table 3). Across countries the two estimates are very similar (r^2 0.913, $p < 0.001$), with the occurrence model generally producing the lower estimates. Total estimates for each of the models ranged from 14.6 to 21.9 million wild boar considering all countries, including those where the wild boar is absent (Ireland has only a few escaped wild boar), recently present and expanding (e.g. Norway, Finland, The Netherlands, UK) or relict (Denmark, Albania), as well as the European part of Russia. When ignoring estimates for these countries to better reflect current distribution range of wild boar, estimates reduced to 13.5 million (occurrence model) and 19.6 million (hunting yield model).

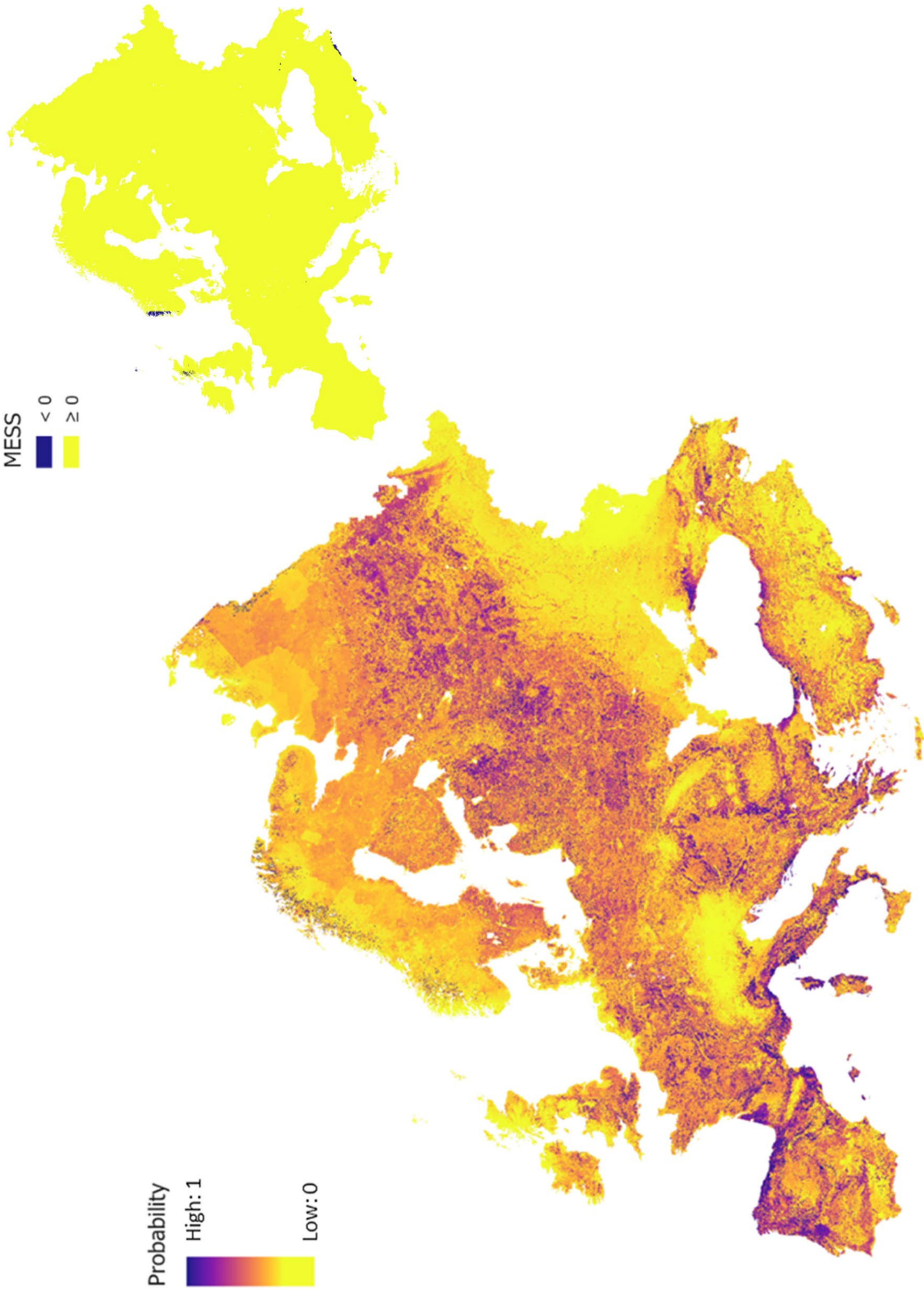


Fig. 5 Map of predicted habitat suitability prior to ASF detection for wild boar at 2 × 2 km. Darker colours denote higher probability. Results of the MESS (Multivariate Environmental Similarity Surface) analysis (top right map), showing the coverage of training data in terms of environmental conditions in yellow and areas of poor predictive ability in blue. Note: predictions were extrapolated to areas beyond the current distribution range of wild boar (Fig. 2)

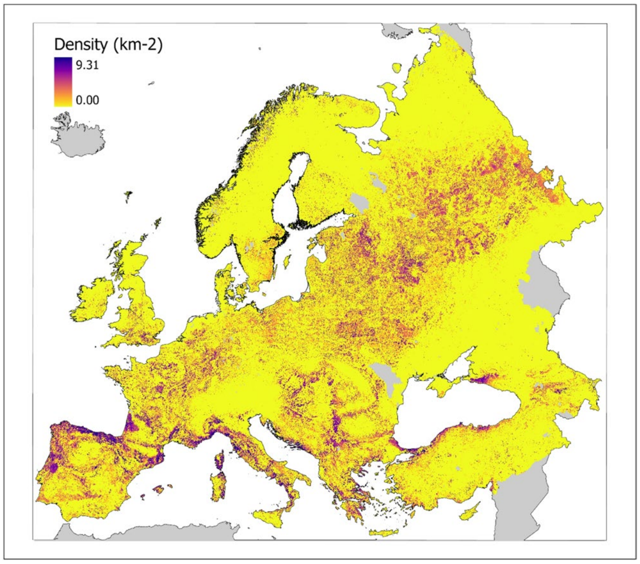


Fig. 6 Predicted wild boar density (2 × 2 km resolution) pre-ASF, or in the absence of ASF, based on occurrence data. Note: predictions were extrapolated to areas beyond the current distribution range of wild boar (Fig. 2)

Although for some countries (e.g. Russia, Slovenia, Switzerland) there were discrepancies in the population estimate according to the methodology applied (Table 3): in general there was a clear association between the estimates obtained by country (Fig. 10).

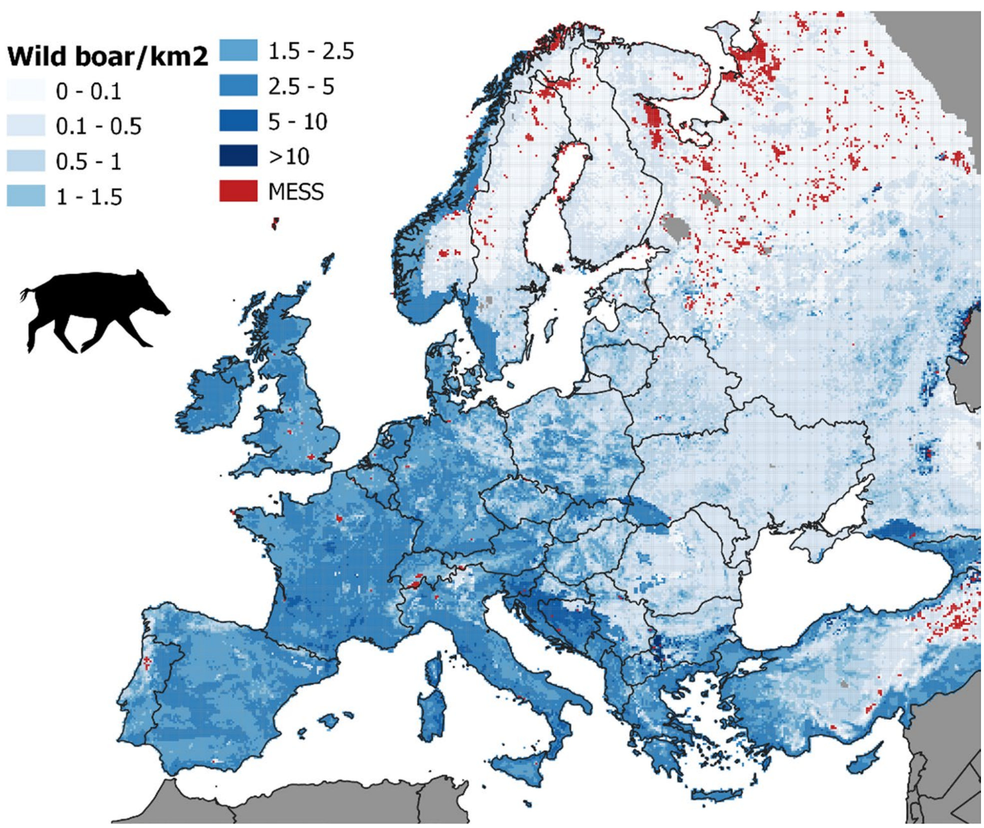
Discussion

This work marks a milestone in wildlife monitoring at the European level. For the first time, to our knowledge, we combined spatial modelling with local density estimates using a harmonised approach to produce calibrated density maps for a terrestrial vertebrate species. This achievement was made possible through a long-term monitoring framework that applies rigorous data quality standards and includes detailed metadata to assess data reliability.

A key enabler of this approach was the development of a European-wide network of "survey sites" under the European Observatory of Wildlife (ENETWILD-consortium et al. 2024b). These sites follow common protocols to generate harmonised and comparable wildlife density data. In this study, we applied updated spatial modelling techniques, based on both occurrence and hunting harvest data, alongside reliable density estimates from across Europe. This allowed us to make two independent estimates of wild boar density and total population by country.

The need for harmonised wildlife monitoring across Europe is urgent. Hunting harvest data suggest a steady increase in wild boar numbers, from 2.2 million harvested annually around 2010 (Massei et al. 2015), to over 3 million by 2017 (Linnell et al. 2020), and nearly 4 million in recent years (ENETwild consortium et al. 2024) despite large local reductions in density

Fig. 7 Predicted hunting yield (individuals per km^2) for wild boar at 10 × 10 km grid but downscaled to 2 × 2 km. Red areas are beyond the environmental domain according to MESS (Multivariate Environmental Similarity Surface) analyses. Note: predictions were extrapolated to areas beyond the current distribution range of wild boar (Fig. 2)



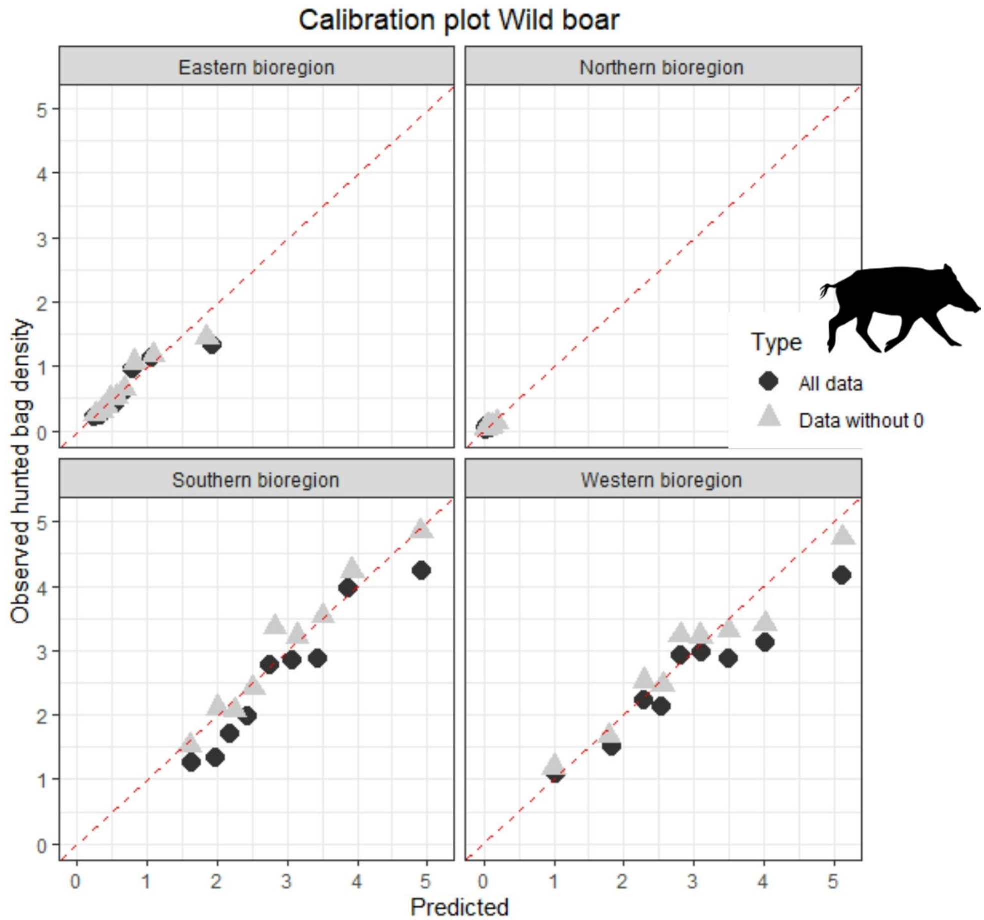


Fig. 8 Calibration plot for assessing predictive performance of wild boar Hunting Yield model for each bioregion of Europe. Plots show the relationship between the predicted hunting yield densities (HY) and the observed ones on the validation datasets

Table 1 Results of the general linear mixed models (GLMMs) for each Spatial resolution showing the Akaike information criterion (AIC) score, R^2 marginal (effects only of fixed factors) and R^2 conditional (effects of both fixed and random factors)

Spatial resolution	AIC	R^2m	R^2c
5 km	162	0.32	0.37
10 km	161	0.32	0.37
15 km	159	0.35	0.40

Table 2 The parameters of the hunting yield model

Intercept	Estimate	t-value	*p*-value
	5.01	4.153	***
log(surface)	−0.47	−3.406	**
log(HYs)	0.59	3.068	**

due to ASF (ENETWILD-consortium et al. 2024a). However, these figures did not previously allow for reliable estimates of total population size. Our methodology, incorporating validated predictions of habitat suitability and relative abundance via hunting harvest, now enables such estimates.

Estimating wild boar density is especially important given the species' continued geographic expansion in Europe despite the localised impact of ASF. Local density estimates, combined with national and continental-scale modelling, provide more meaningful insights than relative indices alone.

These density estimates are valuable for several reasons. Density and thus population estimates provide a baseline to help understand disease ecology, risk, and effects of potential or active management at local, regional, and international levels (Jori et al. 2021). For example, Estonia raised its hunting harvest from 20,000/year to 29,608 animals in the 2015–2016 season as an emergency, with plans to remove approximately 60% females and 40% males and to ban supplementary feeding in key periods. Also, wild boar management for controlling the spread of ASF in the areas called white zones (Lange et al. 2021) require estimating wild boar population to direct efforts, such as in the Belgian case (Licoppe et al. 2023). Furthermore, density and population estimates can be used to help clarify additional ecological, economic, and social impacts of wild boar populations (Barrios-Garcia and Ballari 2012; García-Jiménez et al. 2013)..

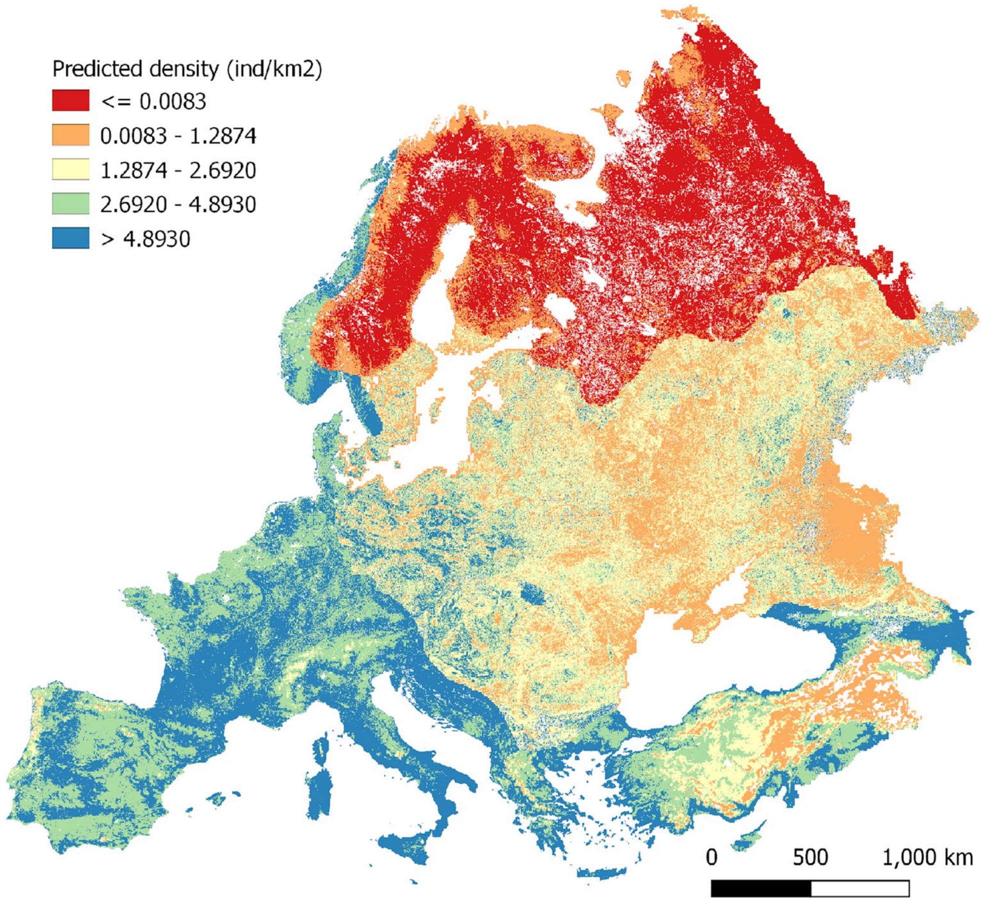


Fig. 9 Predicted wild boar density (2 × 2 km resolution) prior to detection of African swine fever after the calibration of predicted hunting yields-based abundance

The approach

Estimating the absolute population size of terrestrial wild mammals is inherently challenging due to methodological inconsistencies across jurisdictions, including countries. National estimates often rely on different techniques, making them difficult to compare or combine. In this study, we explored two independent approaches to estimate wild boar population density and size across Europe.

The first approach uses occurrence data from the GBIF, collected over many years through citizen science and biodiversity surveys. The second relies on recent hunting yield data, gathered at the finest spatial resolution available. Both datasets were calibrated using robust local density estimates, primarily derived from a consistent methodology applied across Europe (ENETWILD-consortium et al. 2023).

Importantly, these two approaches are entirely independent, with expert input limited to defining the geographic extent of wild boar populations in Europe.

These methodologies have been developed and refined over recent years (ENETwild consortium et al. 2018a; ENETwild consortium et al. 2019; ENETwild consortium et al. 2018c) and represent the best available tools for continental-scale population estimation. While future improvements may allow for integration of these methods, they currently provide the most reliable estimates of wild boar abundance across Europe (ENETWILD-consortium et al. 2024b).

The estimates

The estimated pre-hunting season wild boar population in Europe, prior to detection of ASF, was approximately 13.5 million individuals based on occurrence data, and 19.6 million based on hunting data. These figures exclude countries with minimal or no wild boar presence and do not correspond to a specific year, as ASF first emerged in Georgia in 2007 and reached the Baltic States by 2014, subsequently spreading across Eastern Europe (EFSA et al. 2024; EFSA et al. 2025).

Despite this, these estimates can be considered indicative of the expected population size before 2024 in many countries, assuming stable hunting pressure. As wild boar continue to expand into new regions, such as the UK and Sweden, some national estimates remain uncertain. In some cases, estimates may be skewed due to local factors like intensive population control (e.g., Denmark) or due to limited hunting activity (e.g., Albania).

Table 3 The predicted mean density and calculated population size of wild Boar for European countries prior to detection of African swine fever from models based on occurrence and hunting yield. Hunting data are for the hunting year ending (e.g. 2020/21 is referred to 2021)

Country	Occurrence model		Hunting model		Comments
	Mean density (km^{-2})	Total population	Mean density (km^{-2})	Total population	(maximum annual hunting yield, pre-ASF in the case of affected countries)
Albania*	3.40	**97,817**	5.09	**143,264**	hunting banned since 2014
Armenia	1.70	**50,448**	1.64	**36,540**	No reliable hunting data
Azerbaijan	1.34	**115,612**	No predictions obtained		No reliable hunting data
Austria	0.49	**41,119**	4.80	**396,208**	51,758 hunted in 2022 (ENETWILD)
Belarus	3.73	**773,085**	2.10	**432,108**	48,074 hunted in 2014 (ENETWILD)
Belgium	2.42	**74,231**	4.61	**137,175**	36,390 hunted in 2014, before ASF
Bosnia and Herzegovina	2.99	**152,739**	6.68	**332,933**	3,087 hunted in 2022 (ENETWILD)
Bulgaria	2.80	**311,989**	3.79	**406,330**	45,224 hunted in 2017 (ENETWILD)
Croatia	3.72	**212,433**	5.63	**302,804**	52,381 hunted in 2022 (ENETWILD)
Czechia	1.13	**88,994**	3.96	**305,602**	240,011 hunted in 2020 (ENETWILD)
Denmark*	0.85	**36,881**	4.42	**187,303**	177 hunted in 2022 (ENETWILD)
Estonia	3.61	**164,297**	2.43	**106,989**	32,580 hunted in 2014, before ASF (ENETWILD)
Finland*	0.56	**188,598**	0.08	**23,481**	1,413 hunted in 2022 (ENETWILD)
France	3.15	**1,733,519**	5.54	**3,006,666**	842,802 hunted in 2022 (ENETWILD)
Georgia	1.96	**137,204**	5.66	**348,208**	No reliable hunting data.
Germany	2.11	**755,040**	4.61	**1,625,229**	881,886 hunted in 2020 (ENETWILD), before ASF.
Greece	3.90	**517,142**	5.77	**755,493**	53,488 hunted in 2018 (ENETWILD)
Hungary	2.91	**271,148**	3.36	**312,080**	168,289 hunted in 2019 (ENETWILD)
Ireland*	0.80	**56,490**	No predictions were obtained		Mostly absent, only recent escapes from farms
Italy	3.18	**955,936**	5.85	**1,749,584**	313,080 hunted in 2022 (ENETWILD)
Kosovo	4.32	**46,808**	5.07	**53,361**	Few wild boar hunted and recorded annually (ENETWILD)
Latvia	3.52	**228,036**	2.58	**164,108**	50,956 hunted in 2016 (ENETWILD) when ASF impacted the country.
Lithuania	3.02	**196,530**	2.41	**155,562**	48,317 hunted in 2015 (ENETWILD) before ASF.
Moldova	0.66	**22,356**	1.42	**47,065**	2,623 hunted in 2019 (ENETWILD)
Montenegro	3.16	**42,158**	5.47	**74,450**	1,157 hunted in 2019 (ENETWILD)
The Netherlands*	1.84	**69,275**	5.06	**179,254**	3,793 hunted in 2023 (ENETWILD)
North Macedonia	3.52	**87,706**	4.57	**106,920**	1,893 hunted in 2020 (ENETWILD)
Norway*	0.74	**240,122**	2.06	**597,872**	449 hunted in 2021 (ENETWILD)
Poland	2.55	**797,511**	3.36	**1,048,028**	376,008 hunted in 2020 (ENETWILD)
Portugal	4.31	**395,618**	4.60	**398,820**	37,789 hunted in 2015 (ENETWILD)
Romania	2.04	**485,394**	1.93	**454,465**	52,090 hunted in 2019 (ENETWILD)
Serbia	3.43	**267,955**	2.90	**221,142**	15,228 hunted in 2022 (ENETWILD)
Slovakia	2.34	**114,819**	3.31	**158,215**	75,223 hunted in 2020 (ENETWILD)
Slovenia	0.23	**4,652**	7.14	**137,138**	19,927 hunted in 2022 (ENETWILD)
Spain	3.48	**1,760,443**	4.82	**2,406,359**	434,542 hunted in 2022 (ENETWILD)
Sweden	0.94	**424,252**	0.99	**415,735**	119,972 hunted in 2022 (ENETWILD)
Switzerland	0.13	**5,473**	4.28	**174,207**	14,078 hunted in 2022 (ENETWILD)

Table 3 (continued)

Country	Occurrence model		Hunting model		Comments
	Mean density (km^{-2})	Total population	Mean density (km^{-2})	Total population	(maximum annual hunting yield, pre-ASF in the case of affected countries)
Turkey	1.43	**1,116,278**	3.16	**2,301,372**	No reliable hunting data.
Ukraine	2.07	**1,241,825**	1.83	**1,039,803**	11,167 hunted in 2015 (ENETWILD)
United Kingdom*	1.24	**303,132**	4.65	**1,110,033**	450 hunted in 2019 (ENETWILD).
Total excluding *relict/small populations and/or in limited areas		**13,477,138**		**19,610,699**	This total still includes Sweden, a country at the limit of wild boar range.
Total		14,585,065		21,851,906	

* Total excluding relict populations or where wild boar is only recently present and/or in limited areas, inc. Russia. Azerbaijan was not included since no predictions were obtained for the hunting data model

Although the total population estimate was lower for the occurrence model, it predicted higher populations in north-eastern countries (Belarus, Finland, Latvia) and lower populations across a band of countries from northwest to southeast Europe (including the UK, Denmark, the Netherlands, Germany, Switzerland, Czech Republic, Austria, Slovenia), as well as Georgia, Turkey, and Moldova. These latter countries often fall along the transition zone between low and high densities in the hunting model (see Fig. 4). Notably, some of these countries (e.g., the UK, Norway, Denmark, the Netherlands) lack long-standing, widespread wild boar populations despite suitable habitat, which may also explain discrepancies between the two modelling approaches.

Croft et al. (2025a) highlighted that several European countries (e.g. Switzerland, Austria and Romania) that lacked sufficient occurrence data to reliably model species distributions. These countries span both ends of the data quality spectrum and are not necessarily those with poor hunting data (see ENETWILD-consortium et al. 2021). Therefore, it remains unclear which method, occurrence or hunting data, is more accurate. Each has strengths: hunting data can yield reliable estimates from a few years of records, while occurrence data require longer-term datasets.

The spatial patterns of wild boar abundance derived from hunting data align well with previous studies and ENETWILD reports. Overall, the results are consistent with known wild boar distribution. After European roe deer (*Capreolus capreolus*), wild boar is the most widespread ungulate in Europe, inhabiting a wide range of environments: from forests and scrublands to agricultural areas and high-altitude regions with harsh winters. Yet for species lacking reliable hunting data (e.g. many carnivores, lagomorphs and rodents), occurrence models remain the only viable option to predict spatial patterns of abundance. Therefore, we advocate for the development of harmonized wildlife monitoring systems across Europe to ensure standardized, high-quality data collection—critical for managing ASF and other wildlife diseases for all terrestrial mammals.

In the 2021/2022 hunting season, European countries reported a total wild boar harvest of approximately 3.7 million animals. This figure excludes countries with relict or recently established populations, as well as regions like Russia, the Caucasus, and Turkey, where hunting data are unavailable or less reliable. Since some hunted animals may go unreported or be poached, this is a conservative estimate. Assuming a minimum annual harvest rate of 33%, this implies a population of at least 11.1 million wild boar in these areas. Accounting for underreporting and the presence of wild boar in non-hunted areas, the total population likely falls within the range of 13.5–14.6 million (occurrence model for current distribution and extrapolated to all

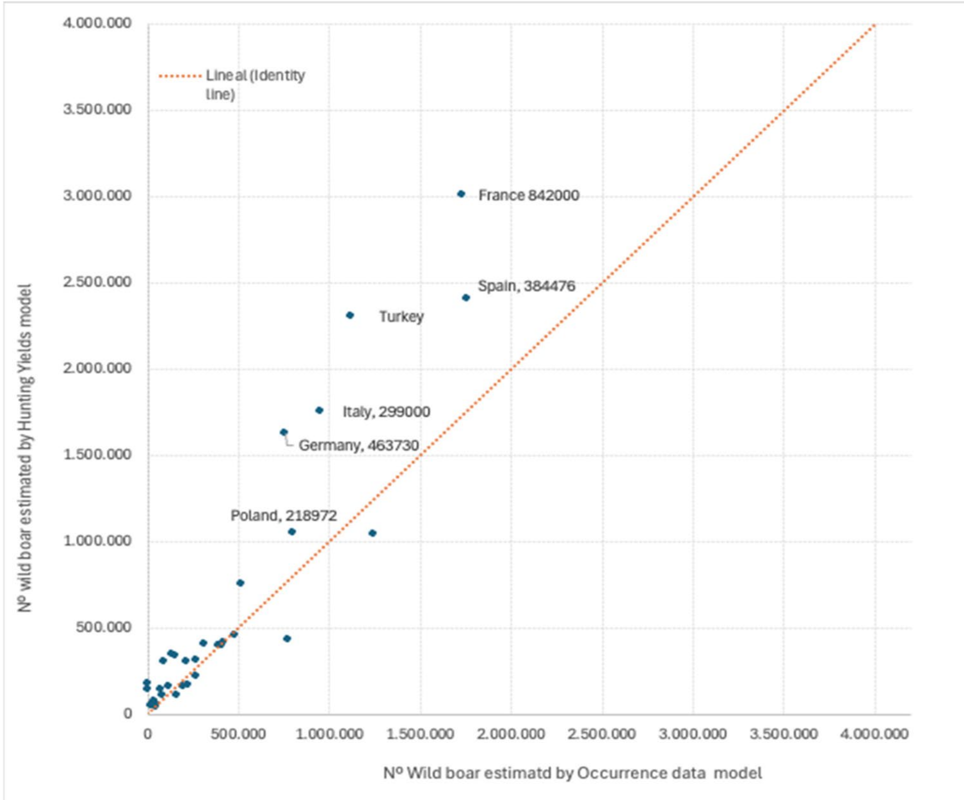


Fig. 10 Association between total population estimates from the hunting model and the occurrence model by country. Relict populations or those only recently present in limited areas, including Russia, were excluded from the analyses. For those countries with higher numbers, the number of wild boar harvested in season 2020/21 is shown (Data provided by Enetwild Consortium, no data available for Turkey)

Europe) or 19.6–21.8 million (hunting model for current distribution and extrapolated to all Europe).

Some density estimates included areas where wild boar are absent (e.g., northern Sweden, Balearic Islands). Models were calibrated using pre-hunting season densities—estimated from late summer to early autumn—when populations have not yet been reduced due to hunting. This may partly explain why some estimates based on occurrence exceed estimates based solely on hunting data.

Density and population estimates should be interpreted on a country-by-country basis, as wild boar distribution, data quality, hunting coverage, and population dynamics vary widely. For example, in Spain—where 85% of the land is legally open to hunting—wild boar are present in nearly all 10 × 10 km grid cells. In contrast, well-established populations occupy less than one-third of Sweden's territory, where the species has greatly increased its range and population during the last two decades.

Despite ASF, the average annual harvest has increased by 4% over the past decade, with about 120,000 more wild boar removed each year (see Fig. 11). As populations continue to grow, our projections based on habitat suitability are expected to align more closely with hunting-based estimates, reflecting the species' full potential in terms of abundance, in the absence of local ASF outbreaks.

Overall, our country-level estimates of total wild boar populations are broadly similar between occurrence and harvest yield models. However, some discrepancies remain between modelling approaches and across specific countries (see Table 3).

A key strength of predictive models is their ability to estimate population sizes across the species' entire range, including areas with limited or no data. One such example in our study is the Caucasus region, where wild boar population dynamics differ notably from much of Europe. In this region, socio-cultural and regulatory factors play a significant role. Ethnic differences in hunting practices have a marked impact: some groups hunt wild boar year-round, placing considerable pressure on local populations, while others refrain from hunting due to cultural traditions, creating localized refuges.

Enforcement of wildlife protection laws also varies widely. Outside protected areas, illegal year-round hunting is common in some countries and may pose a threat to wild boar populations (e.g., current hunting ban in Albania, Ruppert and Trajçe 2018). Even within designated reserves, enforcement is often inconsistent. As a result, models—particularly those based on environmental predictors and maximum hunting yields—may overestimate pre-ASF wild boar populations in some countries. These projections may instead reflect the species' potential population size, which could be reached if current positive trends continue.

We have produced wild boar density estimates for all European countries prior to the emergence of ASF. While

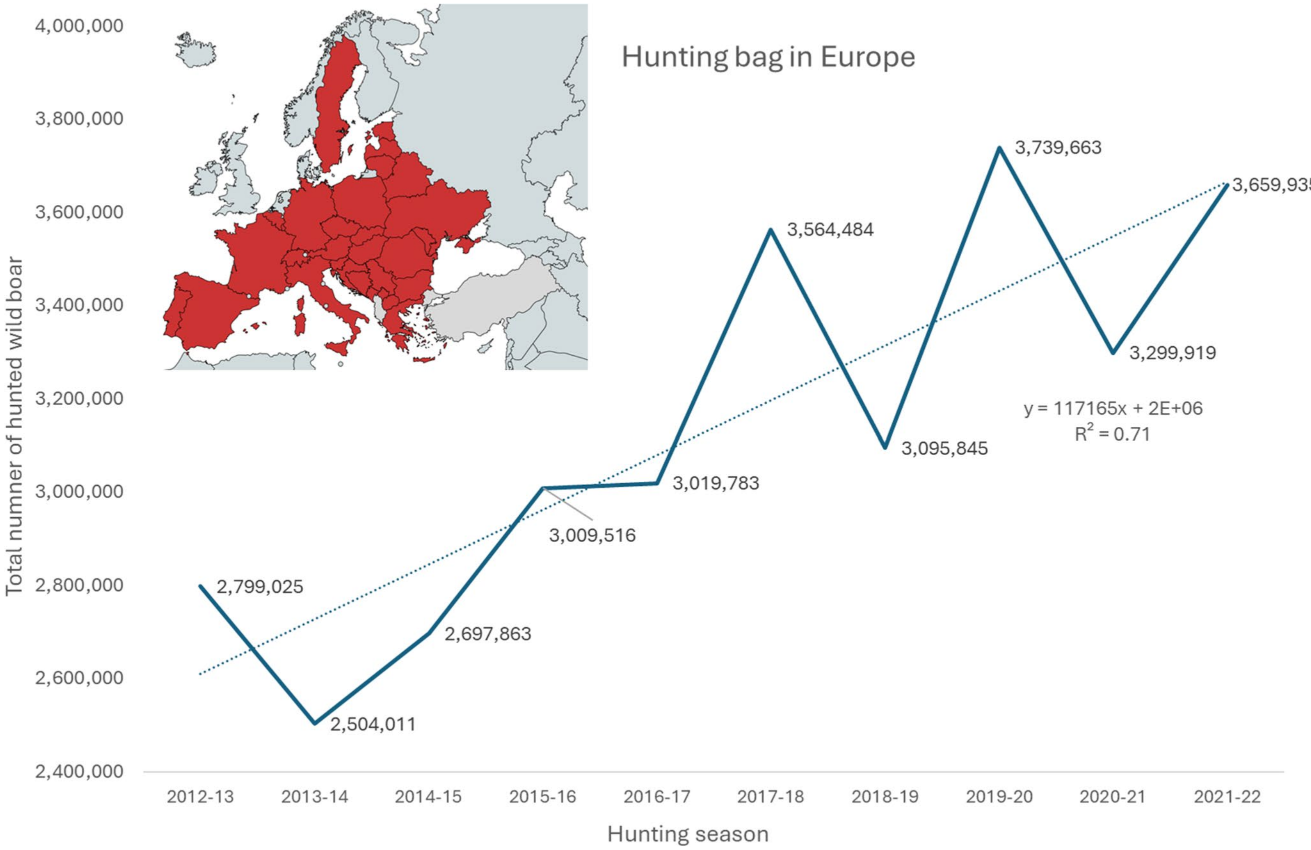


Fig. 11 The wild boar average annual harvest in selected countries, which is still increasing annually by 4% during the last 10 years, about (about 120,000 more wild boar hunted per year (source: ENETWILD data)

these estimates should be refined over time through consistent methodology and thus improved data quality, the next logical step is to assess the impact of ASF on population densities using available data. However, once ASF emerges or is anticipated in a region, hunting typically increases in the short term to reduce wild boar numbers, but may be banned in some areas, rendering hunting-based estimates unreliable in the short term. In contrast, general mammal sighting data are less affected by disease outbreaks, though they require several years of data collection to establish robust relationships between sightings of wild boar (compared to sightings of other mammals) and habitat.

The most reliable approach would be to monitor wild boar densities before and after ASF outbreaks using consistent methodologies. This is one of the goals of the EOW, which aims, using recommended methods (e.g. REM) to include as many study sites as possible and improve their representativeness. Still, given the limited number of sites likely to conduct such monitoring, extrapolating results across Europe will always involve a degree of uncertainty. On the one hand, methods able to derive reliable local population densities tend to be expensive and therefore limit their application to large-scale spatial modelling. However, new technologies (e.g., camera traps), are becoming more affordable with the advantage that the application of information technology tools contributes to reducing the workload for data processing and analysis. This is making the approach increasingly practical and affordable. On the other hand, indicators obtained from information that normally is widely available (e.g., hunting harvest, occurrence) are not always precise enough or can only provide indicators (e.g., population abundance indexes) but offer a comparable overview of the abundance and distribution patterns a large scale. Here we demonstrated the added value of combining both approaches.

This work highlights the urgent need for harmonised wildlife monitoring across Europe to ensure consistent and standardised data collection. Beyond this specific case, our approach demonstrates how calibrated density maps can potentially enhance understanding and management of wildlife disease risk of terrestrial wildlife across the continent for both hunted and non-hunted species.

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Data availability Data is provided within the manuscript or supplementary information files.

Declarations

Competing interests The authors declare no competing interests, except for editorial board members listed as co-authors: Ezio Ferroglio, Stefania Zanet, Pelayo Acevedo, Massimo Scandura.

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