

Short communication

Revisiting wild boar spatial models based on hunting yields to assess their predictive performance on interpolation and extrapolation areas

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ABSTRACT

While reliable estimates of species abundance distribution are required for wildlife management and are greatly needed at broad spatial scales, such information is scarce. In this context, the usefulness of spatial modelling as a tool for predicting game species relative abundance and distribution from hunting yield data was studied. Hunting yield data is affected by several factors related to species management, hunting regulations, and hunting efficacy and some doubts have been raised about the use or reliability of this data for large-scale modelling. Some years ago, Acevedo et al. (2014) calibrated five spatially explicit models (one per bioregion) by using hunting yield data for wild boar *Sus scrofa* (from hunting seasons 2006 to 2009) for approximately 60% of mainland Spain. After internal validation, the models were extrapolated to produce predictions of species relative abundance for the whole mainland country. Here, we reviewed these previous models to evaluate their predictive performance on new data (from hunting seasons 2014 to 2018) in areas where the models had been calibrated (interpolation areas) and also when projected into new ones (extrapolation areas). Our results showed that the previous models were able to forecast current general patterns of wild boar relative abundance with population growth rates equivalent to those reported by other authors, although differences between bioregions were observed. Performance on interpolation areas was higher than that obtained on extrapolation areas. Accuracy of model predictions decreased when fine resolution assessment at hunting ground level was carried out. Our results suggest that spatial models calibrated on hunting yields could be a good option to predict general wild boar relative abundance distribution patterns, although critical assessment is needed, since models can fail when they are extrapolated to areas for which no information is available and at fine scale resolution. These results represent a step forward in the use of hunting yields for describing ranges of species relative abundance at large spatial scales.

1. Introduction

The wild boar (*Sus scrofa* Linnaeus, 1758) is a species involved in numerous conflicts affecting human safety, species conservation and animal health, among others (Melletti and Meijaard, 2017). Reliable estimates of the abundance distribution of this species are essential for sound decision-making. The spread of African Swine Fever (ASF), as an example, has highlighted the need for information on the spatial distribution and abundance of this species for risk assessment (Vicente et al., 2019). Since 2007, more than 10 European Union countries have been affected, with Germany, Greece and Serbia being the latest to report the disease in 2020 (MAPA, 2021; OIE, 2020). The availability of

reliable spatial information about wild boar abundance is greatly needed today to manage and control their populations and disease spread (e.g. O'Neill et al., 2020).

Spatial modelling has become almost the only option employed to produce estimates of game species abundance and distribution at large spatial scales. With respect to wild boar, several models based on both distribution (i.e. occurrences) and abundance data (i.e. number of animals per area unit) have been developed at regional and continental scales in recent years (for a review see ENETWILD Consortium et al., 2018). Many approaches have already been applied to this species in an effort to exploit the wide range of data sources. Depending on the data source, models can be classified into two main categories: those which

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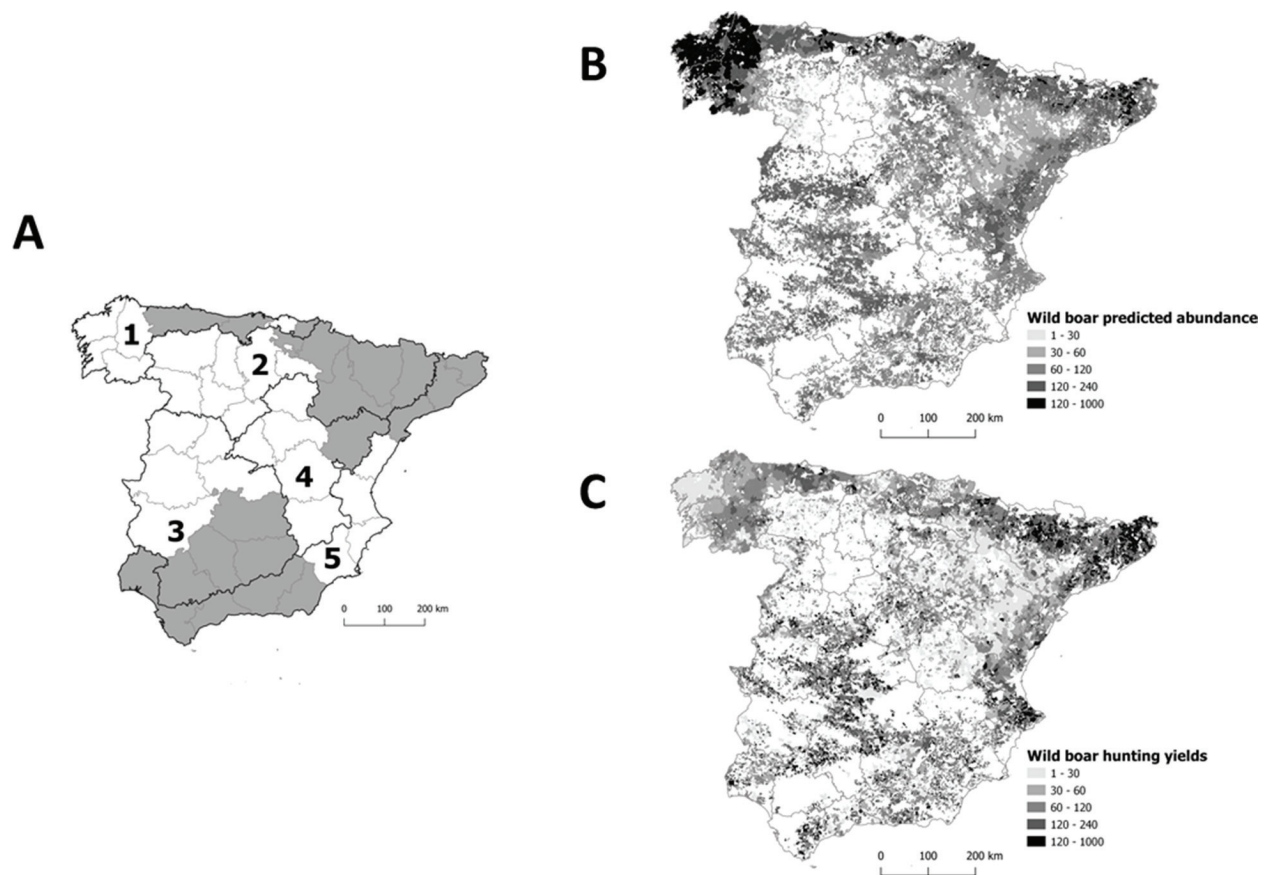


Fig. 1. A) Mainland Spain is divided into the five bioregions defined by the Spanish Wildlife Disease Surveillance Scheme (Internal Report to the Spanish Ministry of Agriculture 2008). Provinces used for model calibration in [Acevedo et al. \(2014\)](#) are highlighted in grey. B) Predicted relative abundance of wild boar (number of animals hunted annually per 100 km²) at hunting ground level according to previous models ([Acevedo et al., 2014](#)). C) New data of wild boar hunting yields (2014–2015 to 2017–2018) used here to assess the predictive performance of the previous models.

use occurrence data to predict environmental suitability (sometimes interpreted as a proxy for the relative abundance of the species) and those that directly model abundance data, mainly hunting yields (namely, the records of the number of animals hunted annually in a given territory). A few remarks should be made about these two categories. In the case of Europe, models based on occurrence data have not produced reliable patterns, mainly due to the lack of presence records in Eastern countries and the lack of reliable absences at continental scale for this ubiquitous species (e.g. [Alexander et al., 2016](#); [ENETWILD Consortium et al., 2019](#)). On the other hand, hunting yield data has been widely explored for modelling wild boar abundance since it usually performs well as a relative abundance index (e.g. [Imperio et al., 2010](#)) and is available for large spatial scales (e.g. [ENETWILD Consortium et al., 2020](#)). However, there are territories that do not record hunting yields, or when recorded, the spatial resolution of the data is variable (from regional scale to hunting ground levels) and hunting pressure may not be comparable between territories (e.g., [Bosch et al., 2012](#); but see [Vajas et al., 2020](#)). Their usefulness for large scale spatial modelling has therefore been questioned (but see [Pittiglio et al., 2018](#)). It should be noted at this point that using spatial models to predict wild boar abundance patterns for large territories is not an easy task nor one that has been resolved (see [Alexander et al., 2016](#)).

Studies assessing the predictive capability of hunting yield-based models on new territories and time periods are scarce but necessary to assess model performance and improve accuracy in results interpretation. Our working hypothesis is that, given that hunting yields are an approximate abundance index, different sources of variability in the data may limit the spatial transferability of hunting yield-based models (bioregion-related factors, for example). To assess this hypothesis, we

revisited the models reported by [Acevedo et al. \(2014\)](#), which were parameterized on data (from hunting seasons 2006 to 2009) for approximately 60% of mainland Spain and then transferred to the whole mainland country (hereafter “previous models”). After testing different modelling approaches, they calibrated five independent models in mainland Spain (one per bioregion) to allow for flexibility in predictor effects and contribution (see Material and Methods section and [Acevedo et al., 2014](#)). Using new hunting yield data (hunting seasons 2014 to 2018), the aim of the present study was to assess the predictive capability of the previous models from [Acevedo et al. \(2014\)](#), looking for differences in performance between territories where the models were parameterized (interpolation area) and projected into (extrapolation area). Specifically, we tested if model predictions produced by Acevedo et al. were able (i) to produce accurate geographic abundance patterns, (ii) to match observed data when a few abundance categories are delimited and (iii) to produce fine scale relative abundance estimates at hunting ground level. These analyses, used as a case study, would make it possible to assess the generalisability of spatial models parameterised on hunting yields and their transferability to non-sampled territories.

2. Material and methods

Five bioregions defined in the Spanish Wildlife Disease Surveillance Scheme (Internal report to the Spanish Ministry of Agriculture 2008) were used for wild boar relative abundance modelling, based on their environmental characteristics and wildlife management practices. [Acevedo et al. \(2014\)](#) considered three approaches to account for potential variation in hunting effort between bioregions: (i) a model fitted with data from all bioregions; (ii) a model fitted using bioregion as a

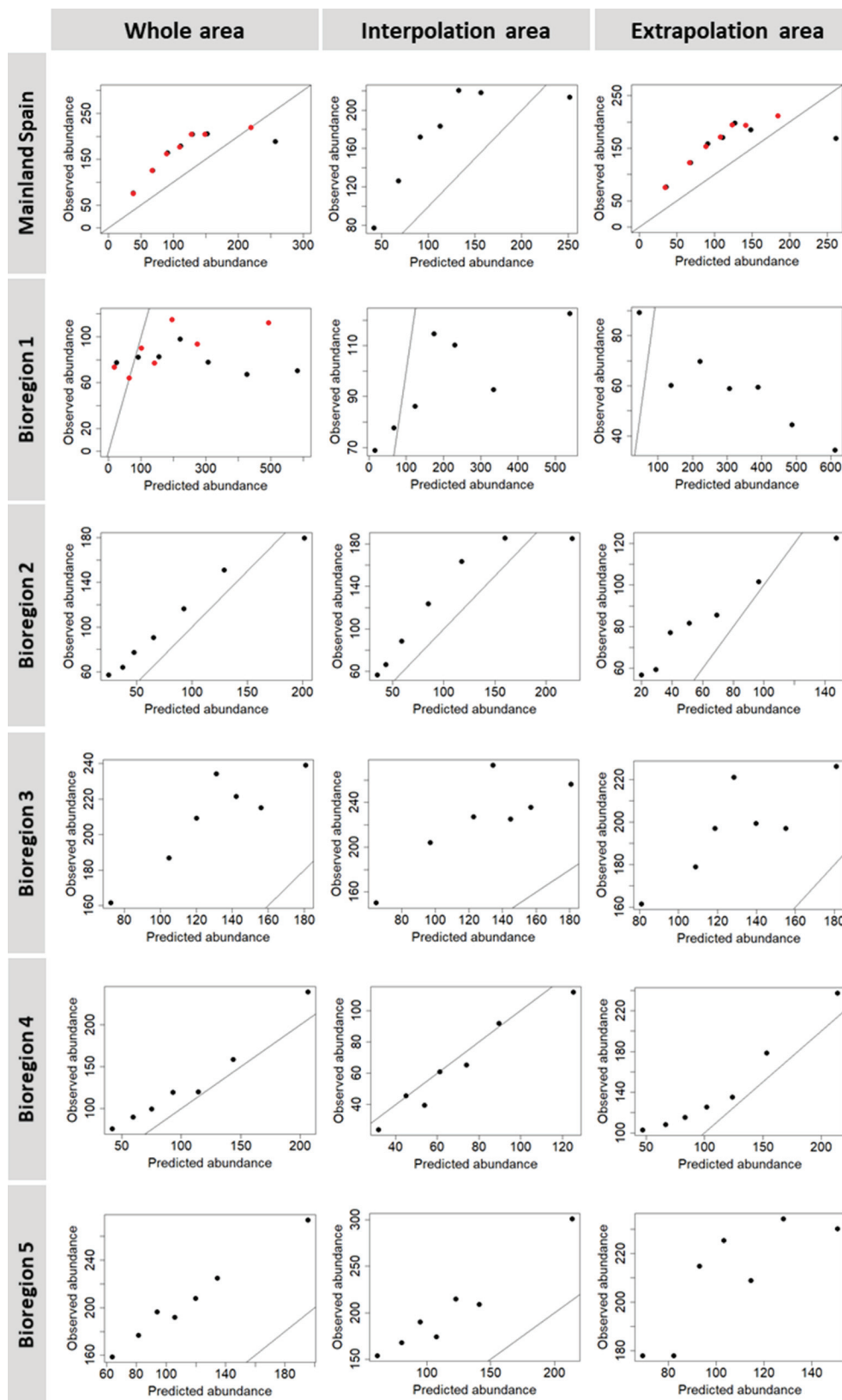


Fig. 2. Assessment of the calibration of the previous statistical models (see [Acevedo et al., 2014](#)) over the whole study area and per bioregion in interpolation and extrapolation areas. Plots show the relationship between predicted and observed wild boar relative abundance on the new datasets. Wild boar relative abundance refers to the number of animals hunted annually per 100 km². Red dots in mainland Spain and Bioregion 1 correspond to the relationship between predicted and observed wild boar relative abundance, excluding the results from Galicia. Solid black lines correspond to identity lines (1:1). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

controlling factor in the model; (iii) independent models fitted for each bioregion. The authors obtained the best performance from approach (iii): five independent models, one per bioregion (see [Appendix 1](#) and [Fig. 1A](#)).

Briefly, the previous models were parameterized by using the mean

number of wild boar annually hunted per 100 km² from hunting seasons 2006–2007 to 2009–2010 as response variable, and a set of 21 predictor variables related to geography, climate and land cover ([Appendix 1](#); [Acevedo et al., 2014](#)). Negative binomial distribution was used for model calibration and a forwards–backwards stepwise procedure based

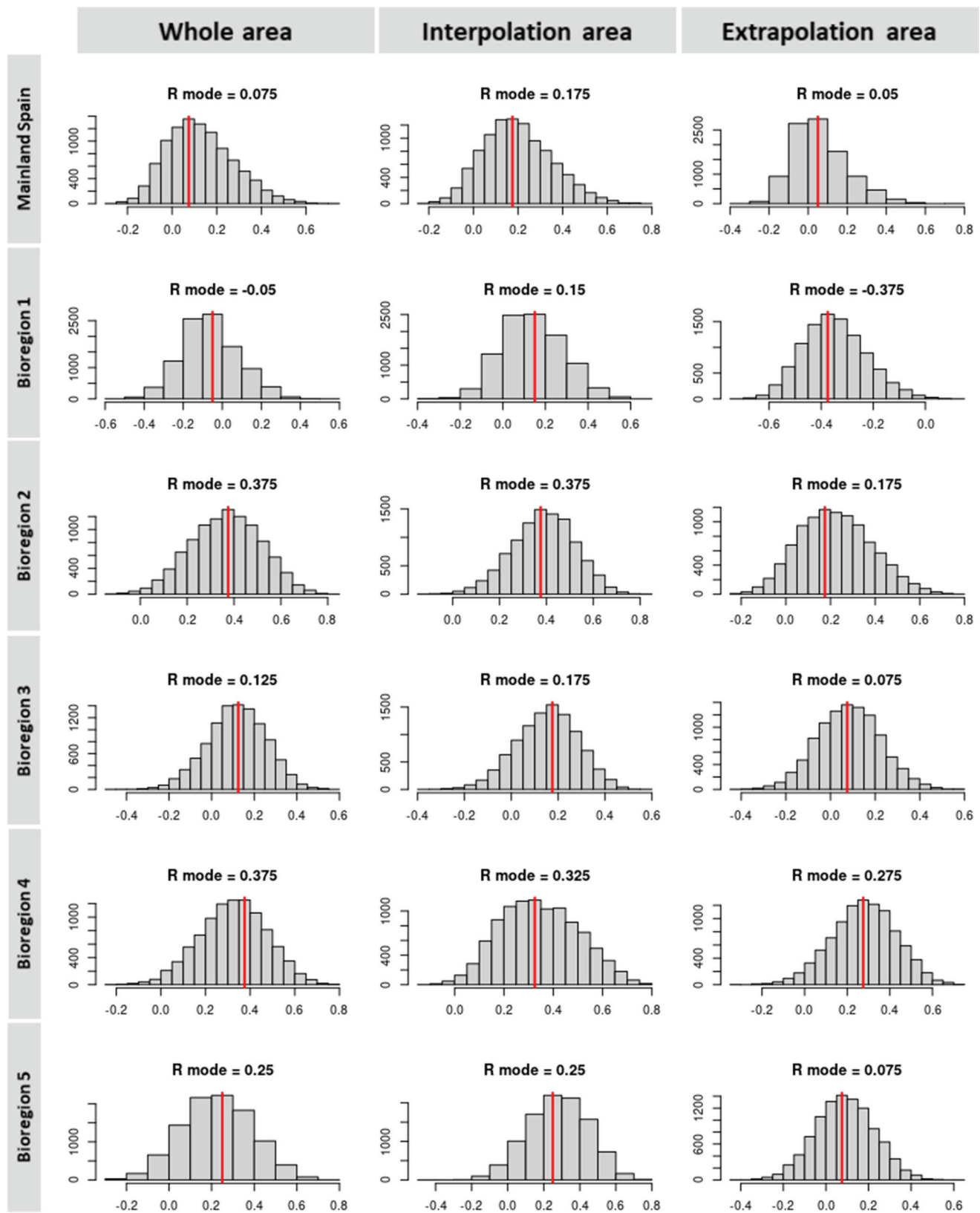


Fig. 3. Results of the subsample procedure for Pearson correlations over the whole study area and per bioregion in interpolation and extrapolation areas. Histograms show r Pearson values from each subsample ($N = 50$, repeated 10,000 times). Red solid line shows the most frequent value (mode).

Table 1

Evaluation of the predictive performance of the previous models (Acevedo et al., 2014) using Pearson correlations and subsample procedure. Mode of Pearson r values is presented. The evaluation was carried out at bioregion level for the overall territory of the bioregion (whole area) as well as separately for territories used to parameterize the previous models (interpolation area, int) and those to which the models were extrapolated (extrapolation area, ext). Finally, the performance obtained by Acevedo et al. (2014) when the models were assessed on independent datasets is also provided.

Bioregion	N° hunting grounds (int / ext area)	Whole area	Interpolation area	Extrapolation area	Performance reported in Acevedo et al., 2014
1–5	13,807 (6797 / 7010)	0.075	0.175	0.05	0.37
1	1,004 (547 / 457)	-0.05	0.15	-0.375	0.54
2	3,061 (1633 / 1428)	0.375	0.375	0.175	0.50
3	3,945 (1777 / 2168)	0.125	0.175	0.075	0.26
4	2,084 (366 / 1718)	0.375	0.325	0.275	0.28
5	3,713 (2474 / 1239)	0.25	0.25	0.075	0.38

on Akaike Information Criteria was used for predictor variables selection. Hunting yield data covered approximately 60% of mainland Spain (Fig. 1A), and model predictions were internally validated on a 20% data subset not used in calibration, and then extrapolated to predict wild boar relative abundance also in non-sampled territories. Modelling approach selection was conducted by correlations between predicted and observed relative abundance in validation data subset.

In the present study, those previous models were used to predict wild boar relative abundance (hunted animals per 100 km²) at hunting ground level in mainland Spain ($n = 13,807$; Fig. 1B). Thus, predictions were obtained from the previous models for territories considered for model parameterization (hereafter the interpolation area) and for those not considered in modelling (without data) to which the models were extrapolated (hereafter the extrapolation area).

We collected recent hunting yield data at hunting ground level for all areas in mainland Spain (Fig. 1C). Specifically, we obtained data for hunting seasons 2014–2015 to 2017–2018, provided by the hunting and fishing services of each autonomous region in Spain. Averaged annual hunting yields (hunted animals per 100 km²; hereafter, observed relative abundance) were used to assess the predictive performance of the previous models.

Model predictions at hunting ground level were performed by solving the model equation (see Appendix 1) at each hunting ground by using the *predict()* function from the “stats” R package. Following Rykiel (1996), we used three approaches to evaluate different features of the predictive performance of models, i.e., if model predictions match observed hunting yields. First, observed and predicted relative abundances were cartographically mapped, in order to visually assess if the geographic pattern of observed relative abundance matched model predictions. Second, we compared observed and predicted relative abundances by using calibration plots, in which observed and predicted values were plotted with bins of fixed size using the *ggplot2* R package (Wickham, 2009). This allow us to determine if model predictions match observed data when a few relative abundance categories are established, and therefore if they produce accurate general abundance patterns. Finally, Pearson correlations were also used to compare observed and predicted relative abundances at fine resolution level (hunting ground level). Calibration plots and Pearson correlations were carried out both globally for mainland Spain and for each bioregion separately. In addition, the interpolation and extrapolation areas used for assessments were disaggregated, and the results were compared for the whole study area and excluding the region of Galicia from Bioregion 1, which had been detected as problematic in the previous models (see below). To avoid misleading P-values in correlations due the high size sample for the most regions, we conducted a subsample procedure to reduce the number of observation in correlations. For each comparison, we randomly subsampled 50 observations and conducted Pearson correlations. We repeated this procedure 10,000 times, storing Pearson r values

and producing histograms to discuss models predictive power and to account for uncertainty in correlations. Then, statistical mode for Pearson r was computed for each comparison.

3. Results

In average, predicted values were 1.35 times lower than the observed relative abundances. Geographical patterns of model predictions are shown in Fig. 1B and the mean of observed hunting yields for hunting seasons 2014–2015 to 2017–2018 are shown in Fig. 1C. Although observed hunting yields were higher than predicted ones, in general similar geographic abundance patterns were found for mainland Spain (but see northwest area i.e. Galicia). Calibration plots for mainland Spain and each bioregion are provided in Fig. 2. Model performance strongly depended on bioregion and interpolation/extrapolation areas. In general, r values from the subsample procedure for Pearson correlations were normally distributed (Fig. 3). Most frequent r values for the subsample procedure ranged from -0.375 (extrapolated area of Bioregion 1, Fig. 3) to 0.375 (whole area of Bioregions 2 and 4 and interpolation area of Bioregion 2, Fig. 3). Standard deviations for all subsamples ranged 0.14–0.15. Table 1 shows the differences in the strength of the relationship between predicted and observed relative abundances at hunting yield level amongst the bioregions, and between interpolation and extrapolation areas in comparison to r values reported by Acevedo et al., 2014.

We found that, in general, model performance was higher when the assessment was carried out in the interpolation areas. Nevertheless, we found differences between bioregions, detecting positive correlations only for bioregions 2 and 4 (Fig. 3).

The exclusion of Galicia region from the evaluation analysis yielded improved assessments of predictive performance for mainland Spain and bioregion 1 (Fig. 2).

4. Discussion

In the short and medium terms, modelling wild boar abundance data is the only feasible option to produce large-scale distribution data of species abundance, which is greatly needed today for population and health management in Europe (Vicente et al., 2019). In this study, we showed that models based on hunting-yield data were able to produce general patterns of wild boar relative abundance over new time periods, and also when used to predict for new territories. Nevertheless, we obtained differences in performance between bioregions and a critical assessment should be carried out before interpreting the predicted patterns. We also showed that while models performed well at large scale, their predictive power decreased at fine scale resolution (hunting ground level).

Predictions from previous models underestimated current hunting

yields (Fig. 1), which could be explained by the growth in wild boar populations in Europe generally, and Spain in particular (Massey et al., 2015). The observed hunting yields were 1.35 times higher on average than those predicted by models parameterized with data from a decade ago. The growth rate obtained in our study is equivalent to 1.5 times the increase per decade that can be derived from the data reported by Massey et al. (2015) for Spain, and 1.7 times the increase reported by Quirós-Fernández et al. (2017) for northern Spain. This provides evidence that the current management of the species has not been able to slow down the expansion of wild boar in recent decades in Spain and that more effective management strategies based on more accurate data are needed to avoid the consequences caused by excess population at different ecosystem scales (Carpio et al., 2021).

In general terms, the previous models were able to predict the spatial pattern of wild boar relative abundance at a national scale (Fig. 1B,C). When the assessment was carried out across the set of bioregions, this trend was much clearer in three of the five bioregions (bioregions 2, 4 and 5), obtaining supports for seven wild boar relative abundance classes as in Acevedo et al. (2014). Pearson correlations at hunting ground level were also stronger for those bioregions (2, 4 and 5, Fig. 3). For bioregion 3, the correlation between observed and predicted hunting yields was fairly lower (Fig. 3), and predicted relative abundance was much lower than observed relative abundance (Fig. 2). This result may have been influenced by hunting management, since hunting estates with perimeter fencing and supplementary feeding predominate in this region and these actions are aimed at maintaining populations even above the carrying capacity of the environment (e.g., Acevedo et al., 2007). Environmental models alone are probably not generalizable enough, since abundance depends more on management interests that can change over the time than on the environmental potential for the species (see also Acevedo et al., 2014). In the case of bioregion 1, the correlation between predicted and observed relative abundance at hunting ground was negative (Fig. 3). Looking for patterns of difference between observed and predicted relative abundance, a high discrepancy was observed in Galicia, which is a region that was not considered for calibrating the previous model (i.e. within the extrapolation area). Even when the performance of previous models on extrapolation areas was not significantly worse than on interpolation areas, the result for Galicia suggests that the previous model of Bioregion 1 was not able to capture the general response of species in this bioregion, and strongly recommends the need to critically assess predictions, mainly when they have potential to be used for management (e.g. Bosch et al., 2017; Vicente et al., 2019). This is a region where *Eucalyptus* spp. is abundant and these plantations can lead to errors in predictions of patterns of wild boar abundance (see ENETWILD Consortium et al., 2020), since *Eucalyptus* plantations are often mapped to resemble forests, although they are not suitable since they are not a favourable habitat for wild boar. We found that when Galicia was excluded from the analysis, the performance of the previous model increased and achieved values comparable to those obtained in the other bioregions (Fig. 2).

In line with our results, when the models were projected over interpolation areas, they predicted the relative abundance of wild boar with some accuracy. This result was expected, as the models showed good predictive power when compared to the evaluation dataset by Acevedo et al. (2014). The previous study found that models were able to predict different classes of wild boar relative abundance and a numerical trend. In this one, we did not find the same relative abundance classes at hunting estate level, but we were able to account for the general spatial patterns. On the other hand, when the predictions of the previous models were compared with observed relative abundance in extrapolation areas, there were differences between bioregions, but returned generally lower performance than in interpolated areas (Figs. 2, 3). In this case, we detected a higher positive correlation between predicted and observed relative abundance in bioregions 2 and 4. These correlation coefficients could be attributed to the representability of the areas sampled in each bioregion when the previous models were

Appendix 1

Table of variables included in the models (generalized linear models with negative binomial distribution and log link function) according to order of entry in the stepwise procedure and table listing variable descriptions below. Hunting bag statistics were used as a response variable and geographical, climate and land cover covariates were used as predictors. All predictor covariates were obtained at 1 km × 1 km resolution. Temporal ranges in predictors comprised 1981–2010. N denotes the number of hunting grounds at interpolation area (I) and extrapolation area (E).

Bioregion	Model
Bioregion 1 N(I/E) = 547/457	$-0.03^*LC3 - 0.04^*LC1 - 0.02^*LC7 - 0.11^*LC8 - 0.9^*TR + 0.001^*P$
Bioregion 2 N(I/E) = 1633/1428	$-0.02^*LC5 - 0.02^*LC6 - 0.01^*LC3 + 0.16^*LON - 0.03^*LC7 + 0.29^*LAT - 0.01^*LC1$
Bioregion 3 N(I/E) = 1777/2168	$-0.01^*LC5 - 0.07^*TJN + 0.02^*HJL + 0.003^*LC4$
Bioregion 4 N(I/E) = 366/1718	$-0.02^*LC5 - 0.01^*LC3 - 0.25^*LON - 0.17^*TR - 0.001^*P - 0.16^*TJN + 0.01^*SR - 0.03^*DFG$
Bioregion 5 N(I/E) = 2474/1239	$0.01^*LC2 - 0.01^*LC5 - 0.01^*LC6 + 0.04^*LON - 0.002^*SR - 0.01^*LC8 - 0.0003^*P - 0.03^*TJL$

Factors	Codes	Variable description
Geographical	LAT	Mean latitude (°N)
	LON	Mean longitude (°E)
Climate	P	Mean annual precipitation (mm) ^a
	DFG	Mean annual number of foggy days ^a
	HJN	Mean relative air humidity in January at 07:00 h (%) ^a
	HJL	Mean relative air humidity in July at 07:00 h (%) ^a
	SR	Mean annual solar radiation (kWh m ⁻² day ⁻¹) ^a
	TJN	Mean temperature in January (°C) ^a
	TJL	Mean temperature in July (°C) ^a
	TR	Annual temperature range (°C) (=TJL-TJN)
Land cover	DFT	Mean annual number of frost days (minimum temperature ≤ 0 °C) ^a
	CI	Continental index ^b
	I	Mean annual insolation (h year ⁻¹) ^a
	LC1	Coniferous forest (%) ^c
	LC2	Broadleaf and mixed forest (%) ^c
	LC3	Scrubland (%) ^c
	LC4	Transitional woodland-shrub (%) ^c
	LC5	Agricultural areas (%) ^c
	LC6	Heterogeneous agricultural areas (%) ^c
	LC7	Pastures (%) ^c
	LC8	Artificial surfaces (%) ^c

^a Source: Font (1983).

^b Source: Font (2000).

^c Source: EEA (2006).

parameterized. Possible causes of the lower correlations in extrapolation areas from bioregions 1 and 3 have been already mentioned above. In bioregion 5 the extrapolation area includes the Community of Valencia, which is a region where there has recently been significant wild boar population growth and expansion, as the hunting yields showed (Lizana et al., 2021). This extrapolation area may not therefore be well characterised according to the sampling carried out by Acevedo et al. (2014).

Wild boar hunting yields are a potential data source for parameterisation of models explaining and predicting relative abundance patterns at large spatial scales. Modelling hunting yields is not an easy task and requires further development to integrate data at different spatial resolutions with different levels of reliability, which is the case today at European scale (e.g. ENETWILD Consortium et al., 2020; Pittiglio et al., 2018). Our results represent a step forward in the use of this kind of data since they support that the models are generalizable and can be used for predicting general abundance patterns over new time periods and large scales. However, caution should be taken when fine resolution abundance estimates are obtained from these models due to differences in hunting efforts, underreported hunting yields, etc. Further assessment of the predictions is required before they can be applied to policy making, especially in the case of wildlife diseases, such as ASF, in which knowledge of the pattern of wild boar abundance is essential to manage

the spread of the disease. (Appendix Table 1)

CRedit authorship contribution statement

Carmen Ruiz-Rodríguez: Data curation, Formal analysis, Visualization, Writing – original draft. **Javier Fernández-López:** Formal analysis, Methodology, Visualization, Writing – review & editing. **Joaquín Vicente:** Writing – review & editing, Funding acquisition. **José A. Blanco-Aguiar:** Writing – review & editing. **Pelayo Acevedo:** Conceptualization, Methodology, Supervision, Writing – review & editing.

Declaration of Competing Interest

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

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Appendix

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