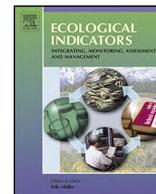


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## Spatial distribution of wild boar population abundance: Basic information for spatial epidemiology and wildlife management



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### ABSTRACT

The Eurasian wild boar (*Sus scrofa*) is growing in numbers and has been expanding its distribution in Europe from some decades ago. This increasing trend, in some circumstances, leads to conflicts involving several sectors, among others, agriculture damages, conservation problems and health risks. The disease-related conflicts are especially relevant; wild boar was raised as a potential host for numerous pathogens provoking economic losses to the livestock industry. In a wildlife management context, reliable indicators of wild boar abundance at large spatial scales are highly demanded. Thus, our main aim was to handle hunting bag data available for the 2006–2007 to 2009–2010 hunting seasons in order to develop a predictive model able to account for wild boar abundance in overall mainland Spain. For modelling, the response variable was the number of wild boars annually hunted per 100 km<sup>2</sup> in each hunting estate, as a well-established wild boar abundance index. Using data for 6280 hunting estates (~44% of the study area), and 21 ecogeographical predictors (geography, climate and land cover), we modelled the species abundance by means of generalized linear models with a negative binomial distribution. Three analytical approaches were comparatively assessed, which differed in how the five bioregions considered in the Spanish Wildlife Disease Surveillance Scheme were considered in modelling. In terms of predictive performance on independent datasets, the approach in which five independent models were adjusted (one per bioregion) achieved the highest scores. These models were used to predict wild boar abundance in overall mainland Spain by using UTM 10 × 10 km squares ( $n = 5245$ ) and municipalities ( $n = 8050$ ) as territorial units, in order to enhance the representativeness of the model at national scale and their usefulness in epidemiological studies, respectively. The pattern for wild boar abundance obtained in this study enlarges the knowledge of this species in mainland Spain. The analytical procedure developed here is valuable in itself, and it can be considered to model the spatial patterns of wild boar – or other relevant species – elsewhere, which is information highly demanded for wildlife managers in general and epidemiologists in particular.

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### 1. Introduction

The Eurasian wild boar (*Sus scrofa*) has experienced a notable growth during the last decades in Europe, both in terms of population abundance (e.g. Sáez-Royuela and Tellería, 1986) and distribution range (e.g. Apollonio et al., 2010). The causes of its expansion are likely related to an elevated ability for occupying

a wide range of habitats (e.g. Abaigar et al., 1994; Acevedo et al., 2006; Schley and Roper, 2003), its prolific reproduction (e.g. Ruiz-Fons et al., 2006) and a generalized increment of food and shelter availability for this species, which was mediated, at least in Mediterranean environments, by the abandonment of the rural areas and the traditional land uses (e.g. Acevedo et al., 2011; Merli and Meriggi, 2006), and the hunting management (Putman et al., 2011). Currently, this species is the most widespread and – generally – also the most abundant wild ungulate in Europe (Apollonio et al., 2010). But this increasing trend, in some circumstances, leads to conflicts involving several sectors, among others, traffic accidents (Lagos et al., 2012), agriculture damages (Herrero et al., 2006), conservation problems (Bueno et al., 2009) and health risks (Gortázar et al., 2007, 2010).

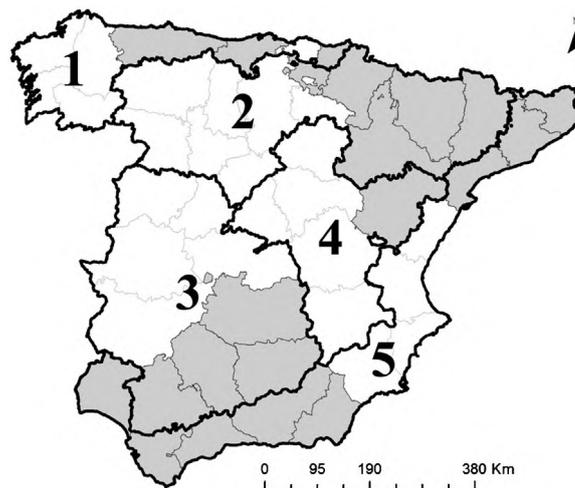
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The relationship between host abundance and health status has been found in numerous studies (e.g. Anderson et al., 1981). High density of wild animals (overabundance situations, *sensu* Caughley, 1981) allows an increase in the transmission of some diseases that can affect not only the fitness of the overabundant species, but also public health and livestock health, as well as the conservation of emblematic species (e.g. Gortázar et al., 2010). In this context, our target species, the wild boar, become a potential host for numerous pathogens (e.g. Ruiz-Fons et al., 2008a), most of them related to shared-diseases (Gortázar et al., 2007). Thus, wild boar has the potential to interfere with the eradication programmes of diseases in livestock. For instance, wild boar is the most important wildlife reservoir of bovine tuberculosis in the Iberian Peninsula (Gortázar et al., 2012), and its population abundance was identified as a relevant risk factor promoting higher prevalences both in wildlife (Vicente et al., 2007) and, at some extent, in cattle (Boadella et al., 2012a). Classical swine fever, the major disease causing economical losses to the pork industry, can be another example. Wild boar may play an important role in the epidemiology of this disease since they can act as a reservoir for the virus and can be a potential source of infection to domestic pigs (e.g. Aubert et al., 1994; Boklund et al., 2008; Laddomada, 2000). Reviewing this disease in wild boar, Artois et al. (2002) linked the wild boar population density to the number of cases and the virus persistence. Similarly, wild boar contact with Aujeszky's disease virus (ADV) remains stable in time in the Iberian Peninsula even after significant reduction of ADV prevalence in domestic pigs (Boadella et al., 2012b), and direct relationships were suggested between wild boar population abundance and ADV prevalence (Acevedo et al., 2007; but see Ruiz-Fons et al., 2008b). This illustrates the increasing risk wild boar pose in the final stages of ADV eradication in pigs, mainly in situations of high wild boar population density.

Under a wildlife management framework in general, and an epidemiological perspective in particular, reliable estimates for wild boar population abundance at large spatial scales are highly demanded in order to establish bases on which management schemes for both the species and the potential diseases can be sustained (Ostfeld et al., 2005). It is well known that wild boar population abundance is not easily estimated because of their complex social structure, nocturnal activity pattern and preference for dense vegetation (e.g. Cahill et al., 2003). So, indirect methods – i.e. methods in which signs of species presence (and no direct counts of animals) are used to estimate population abundance/density – were widely developed and used for this species. These methods include hunting bags analysis (Boitani et al., 1995), pellet counts (Vicente et al., 2004; Acevedo et al., 2007) and, more recently, capture–recapture approaches – for instance, by means of non-invasive genetic sampling (Ebert et al., 2010). The effort required to apply each method is highly variable and it determines their applicability to be used at large spatial scales. On the one hand, generally as sampling effort requirements increase, the method applicability at larger spatial scales decreases (Acevedo et al., 2008). On the other hand, for epidemiologists and wildlife managers, methods requiring little time, cost, and labour are preferred over more demanding methods (e.g. Acevedo et al., 2007). Thus, to estimate wild boar population abundance at large spatial scales, hunting bags statistics are the most recommendable cost-effective and suitable option (Acevedo et al., 2006; Honda and Kawachi, 2011; Sáez-Royuela and Tellería, 1986), since information is available, and this method only requires efforts to systematically register and centralize the information into a database (see Rodríguez-Prieto et al., 2012).

Unfortunately, national/international harmonized programmes to centralize useful information for wild mammals monitoring – as hunting bag statistics – are not yet available (but see [www.aphaea.eu](http://www.aphaea.eu)). For instance, hunting bag data in Spain are recorded at regional level, but raw data digitalized at hunting estate



**Fig. 1.** Mainland Spain, with a division into five large bioregions according to the Spanish Wildlife Disease Surveillance Scheme (Internal report to the Spanish Ministry of Agriculture 2008). Provinces considered in this study are showed (in grey).

level are only available for some regions (e.g. Acevedo et al., 2011); in others only summaries at regional level are produced (e.g. Bosch et al., 2012). In this context, we aimed to manage and process the hunting bag data available for the 2006–2007 to 2009–2010 hunting seasons to develop and validate a predictive model accounting for wild boar abundance in overall mainland Spain. The spatial distribution of wild boar abundance at large spatial scale is highly demanded information potentially useful to understand the spatial epidemiology of shared-diseases, and to identify areas at higher risk for the emergence of undesirable overabundance situations leading to economical and ecological conflicts.

## 2. Material and methods

### 2.1. Study area

The study area was mainland Spain. This is situated in southwest Europe and covers 493,518 km<sup>2</sup> (nearly 85% of the Iberian Peninsula). Mainland Spain is divided into 47 provinces grouped in 15 autonomous communities (regions) which are the administrative units in terms of hunting regulation. Spain is a heterogeneous territory in habitat terms which determines patchy distributions and abundances of wildlife.

Based on habitat features and/or wildlife management, mainland Spain can roughly be divided into five bioregions (Fig. 1) according to the Spanish Wildlife Disease Surveillance Scheme (Internal report to the Spanish Ministry of Agriculture 2008). These bioregions were established in basis to environmental characteristics and, from an epidemiological perspective, the wild species communities and their peculiarities. Muñoz et al. (2010) described the most relevant characteristics of these bioregions. From the perspective of our target species, high abundances are achieved in Atlantic Spain (bioregion 1; Acevedo et al., 2009), distribution ranges of the species are expanding in Northern-Plateau and now is only locally abundant (bioregion 2; Acevedo et al., 2006), intensive hunting management schemes have contributed to high density populations in South-Central Spain (bioregion 3; Acevedo et al., 2007), but only moderate densities occur in the Interior mountains (bioregion 4; Acevedo et al., 2006), and, finally, wild boar is abundant mainly in the northern and southern ends in the South and East coast (bioregion 5; Rosell, 1998).

**Table 1**  
Variables used to model wild boar abundance in mainland Spain.

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

<sup>a</sup> Source: Font (1983).

<sup>b</sup> Source: Font (2000).

<sup>c</sup> Source: EEA (2006).

## 2.2. The data: wild boar hunting yields

The number of wild boar killed in the hunting estates is annually recorded by the regional governments. Standardized by hunting effort, hunting bags statistics are reliable indices of wild boar relative abundance (e.g. Boitani et al., 1995); these indices were validated using data for – very – large time series (Imperio et al., 2010) and also for populations under contrasted hunting management strategies (Acevedo et al., 2007). In this study we used the number of wild boars annually hunted per 100 km<sup>2</sup> in each hunting estate as wild boar relative abundance index. Unfortunately, in Spain, hunting bag data are not routinely included into databases in all regions, and therefore are not easily available for further studies. After contacting with all the Spanish regions, we obtained data (from 2006–2007 to 2009–2010 hunting seasons) for 22 provinces and 6280 hunting estates, that is, for the ~44% of the study area (Fig. 1; data summarized at bioregion level in Table S1).

## 2.3. Environmental predictors

Following the revision of the environmental factors regulating wild boar populations, and based on the accessible information for the study area, we selected 21 variables as potential predictors of wild boar relative abundance (see Table 1). The geographic longitude and latitude were taken into account to reveal geographic trends in the distribution of the wild boar abundance that can be associated with historical events or population dynamics (Legendre, 1993). The relevance of climatic predictors explaining species macroecology is well known (e.g. Acevedo and Real, 2011). Thus, we included 11 climatic predictors assumed to be at least correlated with more explanatory factors. Finally, land use and habitat structure strongly determine wild boar abundance and distribution (see Acevedo et al., 2006, 2009, 2011; Merli and Meriggi, 2006; Virgós, 2002). Accordingly, eight land use-related predictors,

extracted from CORINE database (EEA, 2006), were considered in this study (see Table 1).

## 2.4. Spatial modelling: training, validation and model transferability

Under the circumstance of incomplete information for the whole study area, spatial explicit predictive modelling emerges as a feasible tool from which habitat-species relationships can be adjusted to the surveyed localities, and the statistical models can be used to predict for localities without information of the target species. Thus, a picture of the species abundance for the whole study area can be obtained with this procedure.

The response variable for modelling was the mean number of wild boar annually hunted per 100 km<sup>2</sup> (HY). We pooled data of four hunting seasons (from 2006–2007 to 2009–2010) in order to minimize the potential effect of an unusual year in wild boar hunting yields. Using an inductive approach we determined the macroecological requirements able to predict the HYs at hunting estate level. Predictors were considered in a generalized linear model with a negative binomial distribution and a logarithmic link function (Cameron and Trivedi, 1998), and the final models were obtained using a forwards–backwards stepwise procedure based on Akaike Information Criteria (AIC; Akaike, 1974). We opted for the negative binomial distribution due to high levels of overdispersion in the data when models were fitted with Poisson distributions.

To assess for potential bias due to hunting-related uncontrolled factors at each bioregion, we comparatively developed three modelling approaches: an environmental model for overall mainland Spain (approach 1); a model for mainland Spain, but including bioregion as factor (approach 2); and, finally, five independent environmental models, one for each bioregion (approach 3). If the predictive performance of approach 1 is the highest, then bioregional differences can be derived from the environmental factors. But, if approach 2 attains the highest performance, then differences among bioregions are due to uncontrolled factors, likely related to game management or hunting data recording. Finally, different environmental factors modulate the wild boar abundance in each bioregion if approach 3 reaches the highest performance.

For all approaches, the models were trained using an 80% random sample and model predictions were validated against the remaining 20% of the data. After modelling, wild boar HYs predictions were quantitatively compared with observed data in the validation datasets by using Pearson's correlations, both on the whole study area and independently for each bioregion. These correlations were used to compare the approaches in terms of their predictive performance. Subsequently, the approach with the highest performance was explored in depth for model predictive resolution (Hirzel et al., 2006). This was carried out by plotting the mean observed abundance in each interval of predicted abundance on the validation datasets, and thus perfect adjust points should lie along a 45° line (see Pearce and Ferrier, 2000). Intervals were defined from percentiles. Predictions from models may produce non-linear or staircase shapes in consecutive intervals of predicted abundance. Wherever the local slope between intervals is flat or negative, the corresponding range of predicted values must be pooled into one class without loss of information (see Hirzel et al., 2006). Accordingly, the final predictive resolution of the model's predictions was determined by the number of classes of species abundance that the model was able to predict with precision. These classes of wild boar predicted abundance were taken into account for model transference to the study area (see below).

Three pivotal requirements should be checked before model transference outside the arena of the model, i.e., before the model transference for the whole study area. First, models are not able to accurately predict beyond the range of values of the predictors used

**Table 2**

Variables included in the final models are expressed according to the order of entrance in the stepwise procedure. Coefficients, statistical test-values and significance are in Table S2. Variables coded as in Table 1.

Dataset	Modelling approach	Model
Bioregions 1–5	1	~–LC5 – LC6 – LC3 – TJN – LC7 + LC2 + HJN – TR – P + HJL – LC8
	2	~–LC5 + Bioreg – LC6 – LC3 + LON – TJL + LC2 + HJN – LC8 – P + HJL – LC7
Bioregion 1	3	~–LC3 – LC1 – LC7 – LC8 – TR + P
Bioregion 2		~–LC5 – LC6 – LC3 + LON – LC7 + LAT – LC1
Bioregion 3		~–LC5 – TJN + HJL + LC4
Bioregion 4		~–LC5 – LC3 – LON – TR – P – TJN + SR – DFG
Bioregion 5		~LC2 – LC5 – LC6 + LON – SR – LC8 – P – TJL

for training (Campbell, 2004). For each model, Mahalanobis distances were computing using all localities in the training sample to represent the ecological dissimilarity of the transferring area with respect to the training area, i.e. the degree of extrapolation. Secondly, multicollinearity among predictors in a predictive model can biases model predictions when the model is transferred outside the range where model was trained. We quantified collinearity using predictor's variance inflation factor (VIF). VIFs were calculated – for each predictor and model – as the inverse of the coefficient of non-determination for a regression of a given predictor on all others (see Zuur et al., 2010). Finally, Mantel tests were run to assess the maintenance of the correlation structure of the predictors between the training and the transferring areas (see Jiménez-Valverde et al., 2011). Pearson's correlation coefficient between the elements of the matrices was used as the test statistic and its significance was assessed by permuting the row labels of one matrix relative to the other 9999 times (Manly, 1997). After checking for these requirements, the selected model was used to predict in the whole study area according to its predictive resolution. In this case predictions were carried out on regular territorial units ( $10 \times 10$  km UTM squares,  $n = 5245$ ) in order to enhance the model's representativeness at national scale (e.g. Randin et al., 2006), and also on municipalities ( $n = 8050$ ) as data for livestock is usually aggregated for administrative units (e.g. Allepuz et al., 2011).

Statistical analyses were carried out in R 2.15.2 (R Core Team, 2012). The 'ggplot2' package was used for the calibration plot (Wickham, 2009), 'HH' for the variance inflation factor analyses (Heiberger, 2012) and 'ade4' for the Mantel tests (Chessel et al., 2004).

### 3. Results

Variables included in the three tested modelling approaches are summarized in Table 2 (coefficients, statistical test-values and significance are reported in the Supporting Information, Table S2). When bioregion was considered as a factor (approach 2), it was selected by the stepwise procedure and was significantly retained in the most parsimonious model. According to approach 2, the highest wild boar abundance was attained in the bioregion 3, followed by bioregions 5, 2, 1 and 4, respectively. Some predictors related to land cover (LC5, LC3 and LC6) emerged as the most relevant in the three modelling approaches, since they were included in most of the models at the first steps of the stepwise procedure. The exception was the model for bioregion 1 (approach 3), that is, the Atlantic Spain, where wild boar relative abundance was described by means of different predictors.

When the predictive performance of the models was assessed by relating predicted and observed abundances on the independent datasets, significant Pearson's correlations were obtained for all models (Table 3). Assessing the approaches on the five bioregions all together, we obtained quite similar results from the three tested approaches (Pearson's coefficients: 0.33, 0.34 and 0.37; for the approaches 1, 2 and 3, respectively), being slightly stronger

**Table 3**

Evaluation of the models predictive performance on validation datasets. Wild boar observed abundance was correlated with values predicted from each modelling approach (Pearson's coefficients,  $p < 0.05$  in all cases).

Dataset	Modelling approach		
	1	2	3
Bioregions 1–5	0.33	0.34	0.37
Bioregion 1	0.49	0.51	0.54
Bioregion 2	0.48	0.40	0.50
Bioregion 3	0.20	0.22	0.26
Bioregion 4	0.33	0.35	0.28
Bioregion 5	0.31	0.36	0.38

for approach 3. When the assessment was developed independently for each bioregion the picture was again quite similar among approaches (Table 3), and a clear dominance of one of them could not be determined. Nevertheless, predictions from approach 3 were slightly more accurate for most of the scenarios, with the exception of the results obtained for bioregion 4. Thus, we selected the models from approach 3 for further exploration of their predictive resolution and for transference to the whole study area.

Before transferring the models to the whole study area by using both municipalities and UTM  $10 \times 10$  km grid cells as territorial units, some statistical assumptions were confirmed (see Table 4). Most of the environmental range present in each bioregion was included in the training datasets of the regional models according to the Mahalanobis distance's analyses. Similarly, the variance inflated factors obtained for the predictors included in the regional models showed that no biases predictions are expected due to collinearity-derived problems (VIFs  $< 2.39$  in all cases). Finally, correlation matrices among predictors in the training datasets were maintained in the transference areas according to Mantel tests ( $p < 0.05$  in all cases), which is supporting again of not biased predictions.

As the last stage before the transference of the models, we assessed the predictive resolution (Fig. 2). The obtained calibration plot supports for seven wild boar abundance classes that the model is able to accurately predict. These classes were used for the cartographic representation of the models when were used to predict wild boar abundance for the whole study area (Fig. 3; data at both UTM  $10 \times 10$  km and municipalities scales are available on request to the authors).

### 4. Discussion

From the general interests for wildlife management in determining population abundance at large spatial scales, we successfully developed and assessed a statistical procedure able to predict the abundance of wild boar in the whole mainland Spain (Fig. 3). Obviously, the efforts requested to determine exclusively from field work the abundance of a species like the wild boar at large spatio-temporal scales are unworkable for most of the studies (e.g. Acevedo et al., 2007). Thus, surveying a number of

**Table 4**  
Models transferability assessment: (i) Mahalanobis distance is expressed as the percentage of territorial units (Spanish municipalities or 10 × 10 km UTM squares) within the ecological gradient of the training datasets; (ii) variance inflated factors for the predictors included in the final models (minimum–maximum); and (iii) Mantel tests to check for maintenance of the correlation structure of the predictors between the training and the transferring areas (Pearson's coefficients and statistical significance: \*0.05, \*\*0.01 and \*\*\*0.001).

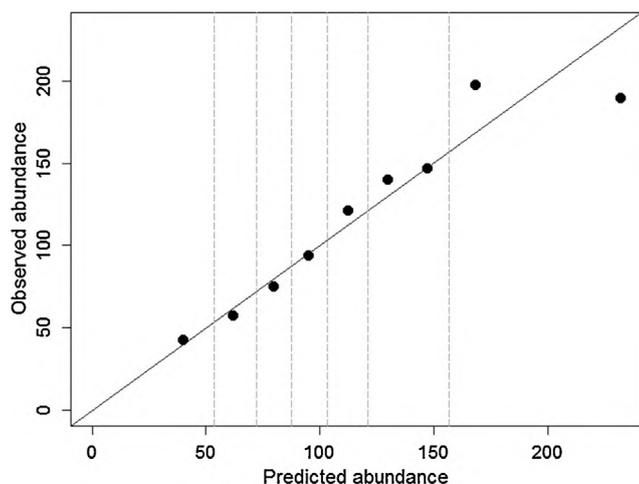
Model	Mahalanobis' distance		Variance inflated factor	Mantel test	
	Municipalities	UTMs 10 km		Municipalities	UTMs 10 km
Bioreg. 1	99.6	98.7	1.18–1.39	0.56*	0.64*
Bioreg.2	99.9	99.9	1.18–2.39	0.67***	0.81***
Bioreg. 3	99.9	100	1.05–1.09	0.66*	0.70*
Bioreg. 4	99.6	99.5	1.16–2.01	0.45**	0.51***
Bioreg. 5	99.9	99.9	1.02–1.78	0.50***	0.62***

representative populations, on which the relationships between species abundance and the environmental conditions can be determined, is a way to forecast the abundance in unsampled territories, by generalizing the adjusted species–habitat relationships. These kinds of predictive modelling procedures are powerful tools for wildlife management, also from an epidemiological perspective (e.g. Acevedo et al., 2010; Etherington et al., 2009).

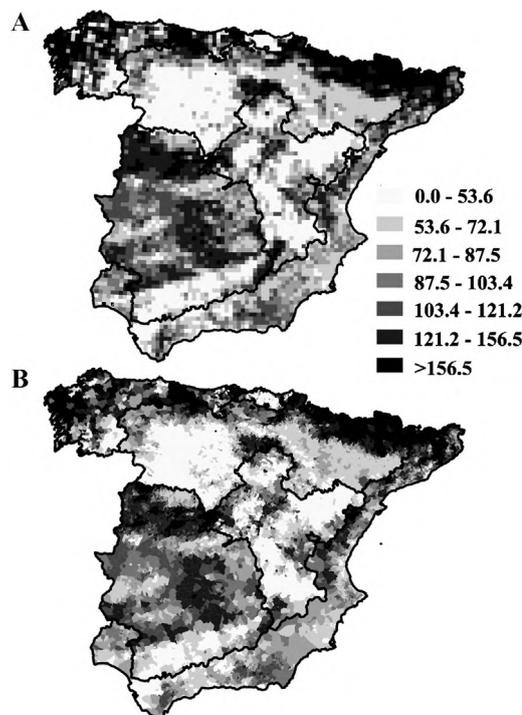
Under this analytical framework, the development of a predictive model of species abundance starts with the selection of the abundance index to be applied in the sampling localities. This selection determines the overall process of modelling and subsequently the accuracy and precision of the model's predictions. In general, the number of sampled localities should be as large as possible and thus, easily applicable methods are preferred for this purpose. For instance, wild rabbit (*Oryctolagus cuniculus*) population abundance at large spatial scales is estimated by latrine counts (e.g. Ferreira et al., 2010). The abundance of badgers (*Meles meles*) in UK at national scale is determined by sampling setts (e.g. Macdonald et al., 1996). For wild boar, even when there are more precise methods to estimate its population abundance (Franzetti et al., 2012), hunting yields are predominantly used at regional/national scales (Acevedo et al., 2006, 2011; Imperio et al., 2010; Rodríguez-Prieto et al., 2012; Sáez-Royuela and Tellería, 1986).

Hunting yields are one of the primary sources of data for game species, but when not corrected by hunting effort, these methods could lead to misleading estimates of population abundance (e.g. Imperio et al., 2010). In this study, we standardized the hunting yields by the surface of the hunting estate (see also Acevedo et al., 2006). In addition, indices based on hunting yields had

been previously validated as wild boar abundance indices in a wide range of wild boar management scenarios that are present in mainland Spain (Acevedo et al., 2007). Even so, these methods should be not exempt from criticisms, mostly in relation to the biases that are potentially introduced from differences in hunting effectiveness and hunting regulation (Acevedo et al., 2009; Bosch et al., 2012; Fernández-Llario et al., 2003). The consideration of the number of hunters involved in the hunting activities, as well as parameters accounting for hunting effectiveness, can improve the accuracy of the wild boar abundance estimation (Acevedo et al., 2009). Unfortunately, this information was only available for a few Spanish provinces, and therefore its inclusion in our study supposed a relevant constraint of the geographical extent in the training areas. Likely, by modelling wild boar abundance data obtained from a more precise method, improved predictions could be obtained; but currently it is not feasible because these data were the best available at national scale in Spain. Standardized protocols for the estimation of wild mammal abundances are not yet produced, as well as networks on which the information from regional/national wildlife monitoring programmes can be centralized. Consequently, an ongoing European initiative is focused on



**Fig. 2.** Calibration assessment of the statistical models fitted for each bioregion (approach 3) and selected to be transferred to the whole study area. Plot shows the relationship between the predicted wild boar abundance for the models and the observed abundance on the evaluation datasets. Wild boar abundance refers to the number of animals annually hunted per 100 km<sup>2</sup>. Dashed lines define the boundaries of abundance classes (predictive resolution) according to the calibration plot.



**Fig. 3.** Wild boar predicted abundance (number of animals annually hunted per 100 km<sup>2</sup>). The statistical models fitted for each bioregion (approach 3) were transferred to the whole study area using 10 × 10 km UTM squares (A) and municipalities (B) as territorial units.

this topic ([www.aphaea.eu](http://www.aphaea.eu)), and high-quality information on population abundance will be available for research and management of wildlife in the coming years.

Results obtained in this study from three modelling approaches pointed out the spatial pattern of wild boar abundance in Spain. A unique environmental model for all bioregions was obtained (approach 1), and its predictive performance was improved by including bioregion as predictor (approach 2; Table 3). This reflects the presence of uncontrolled determinants of the species abundance, operating at regional level. These determinants are probably related to two nonexclusive features: (i) regional differences in hunting regulation and management strategies, that could introduce noises in the abundance indices derived from hunting yields (see below); and/or (ii) a different set of environmental factors could be modulating the abundance patterns in each bioregion (Virgós, 2002). At this respect and accordingly to our expectations, when data for each bioregion were independently modelled (approach 3), we obtained models that achieved slightly better predictive performance than those for approaches 1 and 2 (except for bioregion 4; see Table 3). This can be explained by bearing in mind that mainland Spain is a quite heterogeneous territory (Rivas-Martínez et al., 2004) and the target species is generalist in terms of habitat (e.g. Abaigar et al., 1994; Cahill et al., 2003). Thus, wild boar seems able to exploit different resources across the country (e.g. Herrero et al., 2006). Even when the three approaches were quite similar when were assessed on independent data, we selected approach 3 for further consideration. But, our results suggest that a similar picture of wild boar abundance in mainland Spain that the described from the approach 3 could have been obtained from approaches 1 and/or 2.

We obtained differences in the predictive performance of the models among bioregions (Table 3). Even when model predictions were significantly related to independent data for all cases, the correlation's coefficients obtained for bioregions 3 and 4 were slightly lower than those for the rest. In the case of bioregion 4, this result could be mediated by a small sampling size for model training and validation (Table S1 and Fig. 1). Thus, when more data are available for this bioregion, our model could be updated in order to improve its predictive performance. In contrast, results for bioregion 3 are not expected to be biased by methodological constraints; they could be explained by hunting management: population management is quite intensive in this bioregion (Vicente et al., 2007) and is aimed at maintaining wild boar population over the carrying capacity of the environment in some intensively managed populations (e.g. Acevedo et al., 2007). This action could result in a lack of the predictive resolution of the model mainly in the higher intervals of predicted abundance (see Fig. 2).

Previous studies were focused on predicting the distribution of wild boar population abundance at large spatial scales. For instance, under a framework of human–wild boar conflicts, Honda and Kawachi (2011) modelled both wild boar distribution and hunting yields in order to determine an abundance index of the species and its spatial distribution. These authors obtained higher predictive performance when models were based on presence/absence data, than when based on hunting yields. Nevertheless, the authors realized that a small sampling size could be behind their worse results when modelling the hunting yields. In our study area, three relevant features recommended against the use of distribution models to predict wild boar abundance: (i) the high enough amount of hunting estates with data included in our study (see above), (ii) the wider distribution of wild boar in this country occupying almost the available habitats (e.g. Palomo et al., 2007), and (iii) the results from previous modelling exercises on wild boar distribution (but see Acevedo et al., 2010).

Another study was recently published on this topic; it focused on the Iberian Peninsula (Spain and Portugal). Bosch et al. (2012)

determined the density of wild boar based on the hunting yields at provincial scale. In a posterior step, density was assigned to the suitable habitat in each province in order to approximate how the abundance of the species could be distributed. Nevertheless, the cartographic result is not realistic since the wild boar abundance was considered homogeneously distributed on the potentially favourable areas for the species at province level, which is an oversimplification since nonenvironmental factors (e.g., population dynamics and biotic interactions) also modulate the species abundance patterns (Brown, 1984).

The pattern for wild boar abundance that was obtained in our study (Fig. 3) enlarges the knowledge on this species in mainland Spain providing basic information useful for species management, in a broad sense of the term. For example, including in epidemiological studies the information generated in this study, a more-in-depth understanding of the role of wild boar in the circulation of relevant diseases (e.g. Ruiz-Fons et al., 2008a), and of the potential epidemiological interactions between this species and livestock (e.g. Rodríguez-Prieto et al., 2012) can be obtained. The analytical procedure developed here is valuable in itself, and it can be taken into consideration for futures studies aimed to model the spatial patterns of wild boar abundance in other territories, or of the other relevant wild species elsewhere, which is information highly demanded for wildlife management in general and for epidemiology and disease control in particular.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2013.09.019>.

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