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Deathbed choice by ASF-infected wild boar can help find carcasses

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Abstract

African swine fever (ASF) is a fatal disease infectious to wild and domesticated suids. This disease entered the European Union in 2014 and recently reached western Europe, with the first cases observed in Belgium in September 2018. Carcasses of ASF-infected wild boar play an important role in the spread and persistence of the virus in the environment. Thus, rapidly finding and removing carcasses is a crucial measure for effective ASF control. Using distribution modelling, we investigated whether the fine-scale distribution of ASF-infected animals can be predicted and support wild boar carcass searches. Our results suggest that ASF-infected wild boar selected deathbeds in cool and moist habitats; thus, deathbed choice was mostly influenced by topographic and water-dependent covariates. Furthermore, we show that in the case of an epidemic, it is important to quickly collect a minimum of 75–100 carcasses with exact locations to build a well-performing and efficient carcass distribution model. The proposed model provides an indication of where carcasses are most likely to be found and can be used as a guide to strategically allocate resources.

KEYWORDS

behavioural changes, disease control, distribution model, MaxEnt

1 | INTRODUCTION

African swine fever (ASF) is a fatal disease infectious to wild and domesticated suids. The virus is endemic to the African continent (Montgomery, 1921). In Europe, ASF broke out for the first time in 1957 in Portugal but was quickly controlled. After a three-year silence period, ASF reappeared in Portugal in 1960 and caused a large-scale outbreak (Spain, Malta, Italy, France, Belgium and The Netherlands). Apart from Sardinia, ASF was totally eradicated from the European Union (EU) in the early 1990s. In 2007, however, the virus reappeared on the Eurasian continent in Georgia, from where it has further spread to the neighbouring Russian Federation, Caucasian countries (Armenia and Azerbaijan) and Eastern Europe (Ukraine and Belarus) (Vergne, Gogin, & Pfeiffer, 2017). ASF entered the EU in 2014, first entering Estonia, Latvia, Lithuania and Poland and, more recently, spreading to Bulgaria, the Czech Republic, Hungary, Romania and Belgium (Chenais et al., 2019; Gallardo et al., 2018; Linden et al., 2019).

Carcasses of ASF-infected wild boar play an important role in the spread and persistence of the virus in the environment (Bellini, Rutili, & Guberti, 2016; Chenais et al., 2019; Chenais, Ståhl, Guberti, & Depner, 2018; Torre et al., 2015). Although intraspecific scavenging is not a common behaviour in wild boar (Selva, Jędrzejewska, Jędrzejewski, & Wajrak, 2005), interactions between live wild boar and infected carcasses can represent a serious risk of disease transmission (Probst, Globig, Knoll, Conraths, & Depner, 2017). During the 2017 epidemic in the Czech Republic, the authorities made great efforts to find and remove carcasses, which resulted in the rapid and effective confinement of the disease. Rapidly finding and removing carcasses is a crucial measure for effective ASF control (Chenais et al., 2019; Probst et al., 2017). However, finding wild boar carcasses is a difficult task because carcasses are often consumed by scavengers or hidden under vegetation or snow (Arias, Jurado, Gallardo, Fernández-Pinero, & Sánchez-Vizcaíno, 2017). Although the use of trained dogs (Selva et al., 2005) or financial rewards for hunters can increase the finding efficiency (Gavier-Widén et al., 2015), assisting search teams in their task is urgently needed. Here, we propose a distribution modelling approach using locations of retrieved wild boar carcasses to predict additional carcass locations.

Can we predict the locations of ASF-infected wild boar carcasses from landscape features? Inherent to this question is the assumption that infected animals behave differently from non-infected animals. It has indeed been previously shown that sick animals show a number of behavioural changes, including anorexia, sleepiness and depression, to conserve body resources for the high energetic costs of viral defence (Hart, 1988). Because of these behavioural changes, social animals can become disconnected from their social groups (Lopes, Block, & König, 2016). Moreover, we expect that sick animals will seek particular habitats with conditions that help ease the disease symptoms.

Habitat distribution models are mostly used to predict the impact of climate or land use changes on species ranges (Franklin, 2010). More recently, they have also been applied in the field of disease ecology to predict outbreak risks (Walter, Brugger, & Rubel, 2018). In this study, using a traditional species modelling approach, we aimed to investigate whether the fine-scale distribution of wild boar deathbed choice can be predicted based on previously found ASF-positive carcasses.

2 | MATERIALS AND METHODS

2.1 | Presence data

For model development, we used location data of wild boar found dead during ASF epidemic surveillance programmes in the Czech Republic, Poland and Belgium. In Belgium and the Czech Republic, carcasses were precisely located using GPS, while in Poland, carcass locations were a mixture of precise and estimated GPS coordinates, that is based on descriptions such as nearest village, hunting ground or forest compartment. From these data, we selected carcasses that tested positive for ASF in PCR-based laboratory tests (Linden et al., 2019; Śmietanka et al., 2016; Woźniakowski et al., 2016). In Poland, carcass location was often determined retrospectively by veterinary officers if the sample tested positive for ASF in the reference laboratory. The final set of presence data contained the locations of 603 ASF-positive wild boars found dead: 271 in Belgium, 142 in Poland and 200 in the Czech Republic (Electronic Supplementary Material ESM1).

2.2 | Environmental covariates

We used the following high-resolution and open-source layers from the European Copernicus observation system (Re3data.Org, 2014): forest, grassland, water and wetness (resolution of 20 m); the digital surface model EU-DEM v1.0 (resolution of 25 m); the European settlement map (resolution of 2.5 m); and CORINE landcover data (resolution of 100 m). For the river network, we used the Global River Network data set (Schneider et al., 2017). For linear infrastructure (roads), we used OpenStreetMap with Geofabrik (Ramm, 2017) and the osmdata R package (Padgham, Rudis, Lovelace, & Salmon, 2017) for relevant data extraction (see Table ESM2 for a detailed description of the covariates). We scaled all data sources to a final resolution of 20 m to investigate the process of habitat selection by dying wild boar. Covariate transformation was performed using the raster (Hijmans, 2017) and spatialEco (Evans, 2017) R packages.

2.3 | Modelling approach

We used MaxEnt, a presence-only modelling approach well suited for dealing with low numbers of presence data points (Phillips, Anderson, & Schapire, 2006). MaxEnt is a non-parametric machine-learning approach that contrasts the values of covariates at presence versus background sample points to minimize the relative entropy between them (Elith et al., 2011). The background represents a random sample of the area under investigation. To correct for sampling bias (Kramer-Schadt et al., 2013), 10,000 background points were generated on a bias raster representing the probability of an area being searched for carcasses. During preliminary analyses and based on discussion with local experts, we realized that carcass search sampling was relatively biased in a similar fashion across the countries under investigation. Mostly, the type of habitat (i.e. forest and agricultural areas) and the distribution of linear access infrastructure (i.e. roads and paths) influenced search effort (see ESM3, ESM4).

To account for sampling bias, we used distance to these features to generate the bias raster, with increased probability close to roads and paths and a decreasing probability farther away from forest and agricultural habitats. Background points were then generated over this bias file with corresponding probability values to take into account the uneven sampling effort. Models were trained using 75% of the carcass locations, while the remaining 25% were used for testing, that is evaluating the model. To evaluate model performance, we used two metrics. The first was the threshold-independent area under the receiver operating curve (AUC), ranging between 0.5 (a model with no predictive ability) and 1 (a highly predictive model) (Hanley & McNeil, 1982). The second was the true skill statistic (TSS), a threshold-dependent metric ranging from −1 to 1, where TSS = 0 corresponds to models with no skill to differentiate between the presence and absence of wild boar carcasses in a grid cell (Allouche, Tsoar, & Kadmon, 2006).

We developed three local models, that is one model each for Belgium, the Czech Republic and Poland, and a general model including all data sets. We tested variables for collinearity and removed those with a Pearson correlation coefficient >0.3. Collinearity values between variables were assessed based on the general model, and the remaining set of variables was used for the different models (local and general). This approach enabled us to ensure model comparability and develop simple models based on a limited but relevant number of covariates. The final models comprised the following 7 covariates: heat load index, slope, topographic wetness index, distance to rivers, distance to grasslands, tree cover density and wetness. For each model, we ran 100 repetitions using the same presence data but changing the background data. Models were implemented in the open-source software R (R Core Team, 2018) with the dismo package (Hijmans, Phillips, Leathwick, & Elith, 2017).

2.4 | Do resting sites and deathbeds coincide? A test of the model

We compared our final models with models built using the same set of environmental covariates but with wild boar resting sites as presence data. Resting sites were extracted from GPS tracks. As no tracks were available at the ASF-infected sites, resting sites were extracted from GPS tracks under similar environmental conditions in Belgium and the Czech Republic, namely in Saint-Hubert (57 km north of the ASF epidemic) and Prizer (300 km southwest of the Czech ASF epidemic). We used data from 22 collared individuals (4 in the Czech Republic and 18 in Belgium) tracked between 2005 and 2017. Resting sites were defined as locations at 12:00, when wild boar are known to rest. We obtained 978 and 3,078 resting sites for the Czech Republic and Belgium, respectively, which were used as presence point data to build the alternative models. We reprojected these models into the ASF-infected areas and compared, using a Wilcoxon signed-rank test, the distributions of probability values taken for each pixel.

3 | RESULTS AND DISCUSSION

3.1 | Model performance

To assess overall model performance, we plotted the AUC versus TSS values [16] (Fig. 1). The MaxEnt model outcomes were shown to be robust and showed little variation measured in terms of the standard error of the AUC and TSS. According to the AUC-TSS plot, the Czech (mean AUC = 0.78, mean TSS = 0.47) and the general (AUC = 0.75, TSS = 0.62) models performed best, followed by the Belgian model (AUC = 0.64, TSS = 0.31). The model for Poland performed only slightly better than a random guess (AUC = 0.52, TSS = 0.14). We obtained model performance dependent on the quality of the entry data (Aubry, 2017). The best AUC values were indeed obtained for the Czech Republic, where (a) carcass locations were precisely recorded, (b) survey sampling bias was low due to searches performed in all types of habitats and (c) survey effort was high. In Belgium, locations were also precisely recorded, but searches were mostly focused on forest habitat. In Poland, many of the presence records were unprecise estimates of the locations. This finding highlights the importance of accurately recording carcass locations.

3.2 | Contribution of variables

Our results showed differences in the relative importance of different variables between models. For the general model, slope

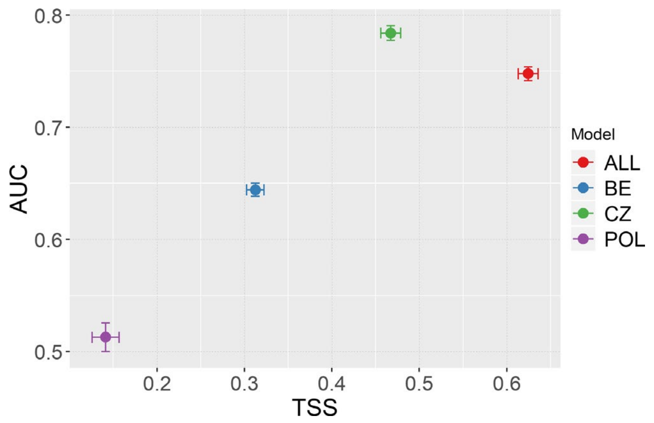

FIGURE 1 Evaluation of the different tested models based on the area under the receiver operating curve (AUC) and the true skill statistic (TSS). Points represent the mean values while horizontal and vertical lines show the confidence interval around that mean, for TSS and AUC, respectively. Model performance increases from the bottom left to the top right corner

(43.1%) and heat load index (41.3%) contributed the most. For the Czech model, distance to rivers (35.8%), topographic wetness (26.5%) and slope (13.3%) were the most influential variables. For the Belgian model, topographic wetness (34.7%), heat load index (23.8%) and distance to rivers (18.6%) were the most contributing variables (ESM5). These results suggest the existence of a habitat preference of dying ASF-infected wild boar. The most influential covariates were composed of topographic variables, suggesting the need for cold, moist and water-rich habitat. Preference for such an environment is a known behaviour of feverish animals. Seeking areas near water and in valleys is a well-known behaviour of healthy wild boar (Kay et al., 2017; Virgós, 2002). Riparian forests provide thermal refuge (Choquenot & Ruscoe, 2003) for species with predominantly behavioural thermoregulation (Bracke, 2011). It is likely that in the case of infected animals with fever, the preference for such habitats will become even stronger than the preference of healthy individuals.

3.3 | Response of variables

We looked at the response curves of the top four contributing variables of the Czech, Belgian and general models. These four variables were heat load index, slope, topographic wetness and distance to rivers. The probability of the presence of ASF-positive carcasses decreased with increasing distance to rivers (Fig. 2). Topographic wetness index had a positive relation with the probability of presence but showed a decrease at very high values. For the Belgian and general models, the probability of presence increased with slope, while for the Czech model, the response was different and presented a bell shape. The response to heat load index (HLI) suggests a relatively high probability of carcass presence in cool areas for the general and the Belgian models, as well as a relative avoidance of really hot areas with HLI > 0.8 (Fig. 2).

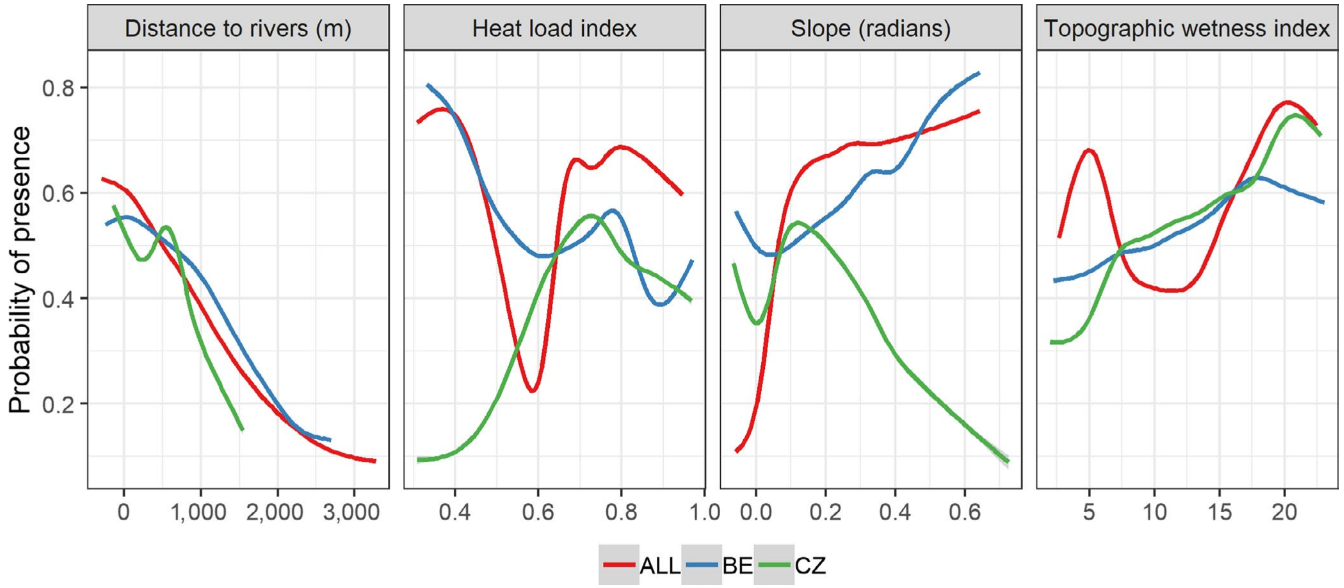

FIGURE 2 Response curves of the four most contributing variables. Heat load index values range from 0 (coolest) to 1 (hottest), while topographic wetness index indicates drainage depressions (high values) and crests and ridges (low values)

3.4 | Sample size effect

Analysis of the effect of sample size on model quality showed that AUC value increases (apart from the Polish model) along with the number of presence points, and this value stabilizes at around 75–100 presence points (ESM6). This result suggests the importance to quickly collect a minimum number of 75–100 carcasses with exact locations to build a well-performing and efficient carcass distribution model at the local scale.

3.5 | Model testing: comparison to wild boar resting sites

For both the Czech and Belgian models, the distribution of resting sites differed from that of ASF-positive carcasses ($p < 0.001$ and $p < 0.01$, respectively), which suggests that ASF-infected wild boar seek conditions different from those of resting sites (ESM7-10).

One way to improve the proposed model would be to include higher-resolution satellite data and micro-habitat variables collected in situ. An infected wild boar might have been found in a particular habitat cell because of micro-habitat conditions not reflected by the coarse-scale conditions of the cell, for example local insolation, visibility, ground-level humidity, an undetectable water stream, a particular micro-relief offering cool conditions or relevant habitat features (e.g. logs or a particular tree understorey). Collecting this information during future carcass searches might be relevant for understanding the role of micro-habitat conditions. We also believe that seasonal changes in weather conditions (e.g. the presence of snow) could diversify the selection of dying sites by ASF-infected wild boar throughout the year. However, we did not take this seasonality into account since we had no accurate information on carcass age, which would have been necessary to properly assign carcasses to season. Including carcass age at the time of detection could therefore be of high interest. It is also important to note that recent but not yet published results suggest that some wild boar may carry ASF infection in subacute form. These wild boar which present a high potential to spread the virus for a long period of time are not suffering from the ASF symptoms and therefore do not fulfil our baseline assumption (ASF-positive individuals behave differently than healthy one).

We provided the first model on the distribution of carcasses of ASF-positive wild boar. The proposed model can provide indications of where carcasses are most likely to be found and can be used as a guide to strategically allocate resources. However, we recommend that locally adapted models be developed as soon as enough data on ASF-infected carcass locations are collected. Our results suggest that it is important to quickly collect a minimum of 75–100 carcasses with exact locations to produce a model that can be used to guide subsequent searches. However, until that point, the general model presented here can be applied as it was found to provide results comparable to the model that performed best.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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