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Future distribution of wild boar in a highly anthropogenic landscape: models combining hunting bag and citizen science data

Rutten, Anneleen[1,2*]; Casaer, Jim[2]; Swinnen, Kristijn RR[3]; Herremans, Marc[3]; Leirs, Herwig[1]

[1] Evolutionary Ecology group (EVECO), University of Antwerp, Universiteitsplein 1, B-2610 Antwerp, Belgium

[2] Research Institute for Nature and Forest (INBO), Havenlaan 88 bus 73, B-1000 Brussels, Belgium

[3]Natuurpunt Studie, Coxiestraat 11, B-2800 Mechelen, Belgium

***Corresponding author: anneleen.rutten@uantwerpen.be**

Highlights

- MaxEnt models using sampling bias correction based on citizen science data
- Future wild boar distribution in a highly anthropogenic landscape
- Wild boar have a high behavioral flexibility to adapt to human-dominated landscapes
- Forest, maize, scrub and low natural cover play a key role in defining habitat suitability

Declarations of interest: none

Author contributions

- Rutten Anneleen: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, visualization, writing- original draft
- Casaer Jim: conceptualization, writing- review & editing, funding acquisition, investigation
- Swinnen Kristijn: data curation, formal analysis, methodology, writing- review & editing
- Herremans Marc: writing- review & editing, methodology
- Leirs Herwig: writing- review & editing, funding acquisition

ABSTRACT

Wild boar is one of the most widespread mammals of the world and in many regions wild boar populations continue to expand. Especially in highly anthropogenic landscapes, increasing numbers of wild boar lead to a rising number of contacts with human activities causing human-wildlife impacts. In the heavily fragmented landscape of Flanders (northern Belgium) where the wild boar re-appeared in 2006 after more than half a century of absence, it is crucial to get a better understanding of the probable further distribution of wild boar in order to assess potential impacts in the near future. Wild boar occurrences have been collected by two citizen science programs: through an online observation platform and based on the reported locations of wild boar shot by hunters. This allowed us to construct a MaxEnt habitat suitability model. We constructed a new approach to define background manipulation to correct for sampling bias due to uneven sampling effort or due to areas in which hunting is not allowed based on the construction of bias files using this information. Model outcomes based on this new approach for background manipulation were compared with the known method of spatial thinning. All model outcomes were found comparable reflecting the utility of our new approach when limited data are available and spatial thinning would result in insufficient data for modelling. Our MaxEnt models show that coniferous forest, deciduous forest, maize, scrub and other low cover play a key role in increasing the habitat suitability for wild boar. Built up areas and the extent of habitat diversity only had a minor influence on habitat suitability reflecting wild boars' behavioural flexibility to adapt to human-dominated landscapes. Unoccupied suitable habitat is mainly found in the centre of Flanders, although highly scattered. Habitat suitability in the West of Flanders was limited.

Key words: *Sus scrofa*, MaxEnt, Species distribution modelling, citizen science, sampling bias

1. INTRODUCTION

Landscapes are becoming increasingly anthropogenic and fragmented, causing wildlife to come more into contact with human activities (Barua et al., 2013; Messmer, 2000). Human-wildlife impacts (HWI, here defined according to Redpath et al. (2013) as impacts due to interactions between wildlife and human activities) are the main limiting factors in acceptance of wildlife by stakeholders (Carpenter et al., 2013). Wild boar (*Sus scrofa* L.) related HWI are increasing since the 1960's when wild boar populations started to expand and increase throughout the original native range in Europe and in other parts of the world where feral wild boar are non-native (Massei et al., 2015; Mayer, 2018; Saez-Royuela and Telleria, 1986). These population expansions resulted in wild boar becoming one of the most widespread mammals in the world (Keuling et al., 2018). HWI involving wild boar include damage to agricultural crops, traffic collisions and disease transmission (Bieber and Ruf, 2005; Morelle et al., 2016; Treves et al., 2006).

In Flanders (northern Belgium), wild boar disappeared after the second world war due to overhunting. However, since 2006, after more than half a century of absence, wild boar re-emerged in several locations. In the Eastern province of Limburg they reappeared in two geographically distinct locations. These founder populations were geographically not connected to populations abroad excluding natural recolonisation by migration; however there is no confirmed information on the origin of these populations (Rutten et al., 2019). Since their return, both population numbers and distribution ranges are increasing but the distribution is currently still mainly limited to the North-East of Flanders (Scheppers et al., 2014). During the last decennia, the Flemish landscape altered substantially due to economic growth, urbanisation and agricultural intensification. Currently Flanders is one of the most densely human populated areas of Europe (Linell et al., 2001), characterized by a severely fragmented landscape and an intense intertwinement of agricultural, natural and urban areas. As a consequence wild boar presence results in an increasing numbers of HWI. By getting a better understanding of factors determining habitat suitability for wild boar, the habitat suitability of currently uncolonized areas can be estimated, returning crucial information for conducting a risk assessment related to future potential wild boar expansion. Conducting such risk assessments allows to develop effective management strategies in order to avoid HWI's (Červinka et al., 2015; Fischer et al., 2015).

Distribution models play an ever increasing role in conservation planning, wildlife management and related decision-making (Araujo and Guisan, 2006; Kozak et al., 2008; Warren et al., 2014). Species distribution models (SDMs also called Habitat suitability models (HSM, Bellamy et al., 2013) or Ecological niche models (ENM, Sillero, 2011)) relate species occurrences to environmental variables, thereby creating insights into habitat suitability for the species in question (Elith and Leathwick, 2009). Characterizing the distribution of species does not only provide ecological insight but also allows to predict distribution across space and/or time (Elith and Leathwick, 2009). These predictions

may concern effects of climate change (Khanum et al., 2013), invasive species distribution potential (Bradley et al., 2010) or recolonisation of native species (Swinnen et al., 2017). The use of models already showed its utility in wildlife management in the past (Baldwin, 2009; Saito et al., 2012).

SDMs should be based on the understanding of the species biology, ecology and impact of human disturbance (Araujo and Guisan, 2006). Various studies assess habitat suitability for wild boar in Europe (Bosch et al., 2014b; ENETwild consortium et al., 2019; Morelle et al., 2016). These studies mainly report forest to be among the most important factors determining habitat suitability. Furthermore, agriculture was found an important factor enhancing habitat suitability due to (seasonal) food availability and shelter opportunities (Herrero et al., 2006). Wild boar also prefer the presence of water in their home ranges (Ilse and Hellgren, 1995). Wild boar show a substantial behavioural plasticity in adjusting to human-dominated environments (Stillfried et al., 2017a) and even became habituated to metropolitan areas like Barcelona and Berlin (Cahill et al., 2012; Kotulski and König, 2008). However, their spatio-temporal behaviour has been found to be affected by human presence (Podgórski et al., 2013). Human interference and open vegetation without shelter opportunities have been reported to negatively impact the suitability of an area (Alexander et al., 2016; Bosch et al., 2014a). Moreover, even in urban area, natural food sources are, when available, preferred over anthropogenic food sources such as garbage (Stillfried et al., 2017b). Previous landscape genetic studies in Flanders and Wallonia showed no clear effects of forest fragmentation or fragmentation due to roads on landscape connectivity for wild boar (Dellicour et al., 2019; Rutten et al., 2019) although more continuous, less fragmented landscapes are suggested to be more suitable (ENETwild consortium et al., 2019). The Flemish landscape is one of the most extremely fragmented and anthropogenic areas in Europe. Therefore, Flanders provides an interesting case study for understanding wild boar expansion mechanisms in extremely fragmented landscapes and to assess if there are limits towards wild boars' behavioural plasticity in adjusting to anthropogenic pressures.

Species occurrence data are essential in SDM. Citizen science data are numerous and have been shown to advance knowledge of species occurrences and their distributions (Bonney et al., 2009), e.g. as a basis for SDM's (Crall et al., 2015; Mair et al., 2017; Swinnen et al., 2017). In Flanders, wild boar observations of the data portal www.waarnemingen.be of Natuurpunt (Swinnen et al., 2018) provides a dataset that can be used in a SDM. Another citizen science data source of wild boar occurrences comes from Flemish hunters. Hunting bag data have already been suggested to be useful in SDM, however they are often recorded at too low resolution (ENETwild consortium et al., 2019). Given that Flemish hunters have the possibility since 2016 to register the exact coordinates of the location where individual wild boar were shot, a SDM approach at a detailed resolution is possible with these data.

The first aim of this research is to use SDM to gain a better understanding of the factors influencing habitat suitability and therefore determine the potential future distribution range of wild boar in the

highly anthropogenic landscape of Flanders. The results from this research forms an essential element in risk assessments to evaluate potential impacts when wild boar expand further into this severely fragmented and anthropogenic landscape.

Sampling bias can however affect the results of SDM's (Guillera-Arroita et al., 2015): this bias can be related to uneven search effort, reporting behaviour or variation in detectability of the target species across the landscape. This can lead to localities that are biased in environmental space due to spatial autocorrelation of recorded species occurrences (Boria et al., 2014). By correcting for sampling bias, model over-fitting is avoided. There are some proposed methods which can be used to correct for sampling bias (e.g. spatial thinning or background manipulation with bias files (Boria et al., 2014; Kramer-Schadt et al., 2013)). This background manipulation using bias files is often based on occurrence data of similar taxa. Our datasets allowed a new approach to define bias. The online portal of waarnemingen.be contains observations of many species; Using the observation characteristics of wild boar observers, we designed a method to define search effort. Moreover, as we have detailed maps of hunting grounds, we are able to assess sampling bias in hunting bag data due to the fact that hunting does not take place everywhere. Both search effort as hunting effort (based on hunting grounds) lead to the development of bias files to adjust background selection so sampling bias is taking into account. Based on this new approach defining sampling bias, as a second goal of this study we will assess how well our two approaches perform compared to spatial thinning to correct for sampling bias. With increasing number of citizen science data collections, our new approach can be of importance to take sampling bias into account when using this kind of data for modelling purposes.

2. METHODS

2.1 Study area

Flanders has a surface of 13 587 km² and has a cool temperate and moist climate (Metzger et al., 2013) with an annual average temperature of 9.7°C and 800 mm rainfall. Flanders has mainly a flat or gently undulating landscape from sea level in the west to 150 m above sea level in the South and East. The Flemish landscape is highly fragmented with only 11% forests, 53% agricultural land, 30% build up areas and the remaining 6% consists of water, swamps, heathlands, natural grasslands, estuaries and dunes (Demolder et al., 2014). An intense intertwinement of natural, agricultural and urbanized areas is crossed by a dense road network (5.08 km/km², Vercayie and Herremans, 2015). The current distribution area of wild boar is mainly limited to the eastern provinces of Limburg, Antwerp and Flemish Brabant but their distribution range is expanding towards the centre (Figure 1). Current neighbouring wild boar populations are found in the Netherlands near the Belgian border and in Wallonia (Rutten et al., 2019).

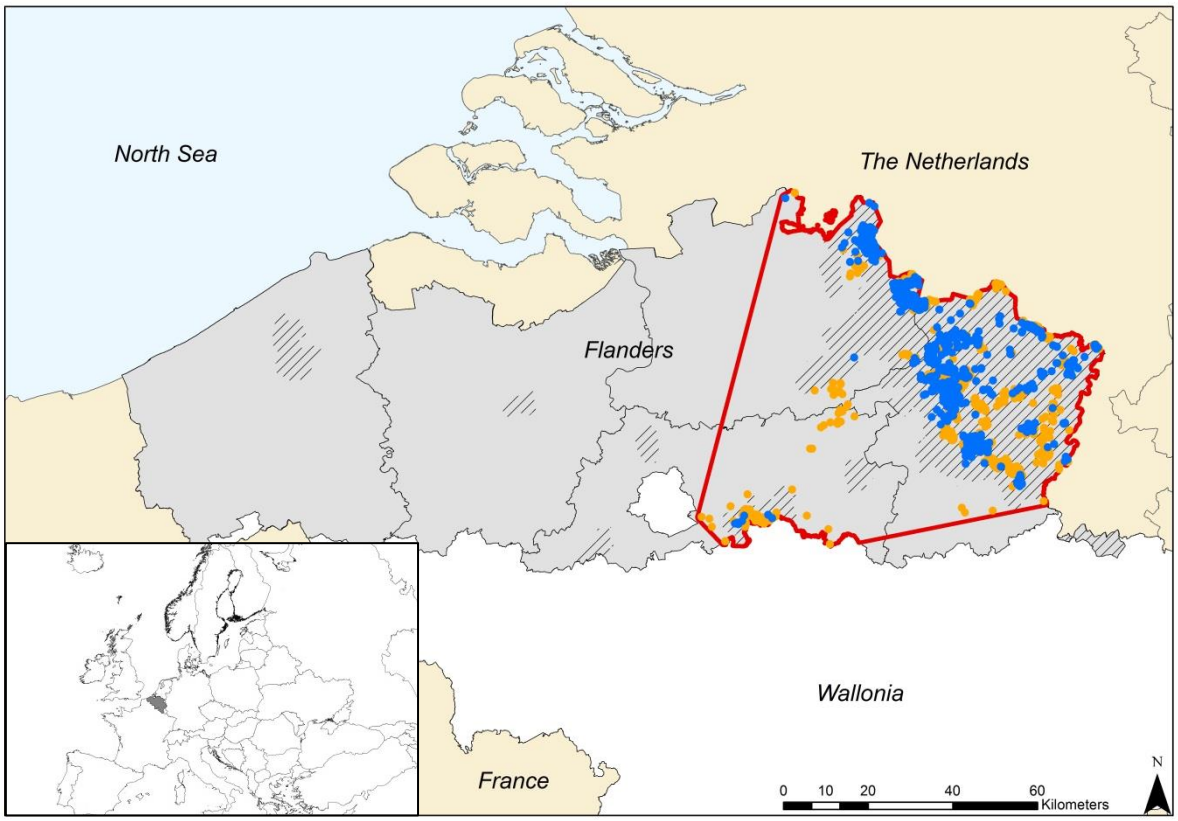

Figure 1: Study area of Flanders (grey) with 1383 occurrence records from waarnemingen.be (orange) and 1510 locations from hunting records in the eastern provinces (blue) and current distribution range of wild boar (dashed area, based on hunting records at municipal scale for 2018). The red polygon is the minimum convex polygon encompassing the data records used for MaxEnt background selection.

2.2 Data collection

Citizen science data on wild boar presences in Flanders was obtained from two different sources. Firstly the website waarnemingen.be, a portal of citizen scientist's records of plant- and animal species in Belgium which started in 2008, containing over 33 million observations. The goal of waarnemingen.be is to be the digital notebook of all nature observations for users. The collected biodiversity information is shared with the public and species specific maps and statistics are reported. The data is used to gain information on species occurrences (Steeman et al., 2017), to monitor biodiversity or is used in species specific research projects (e.g. Swinnen et al., 2017). Records include sightings, footprints, rooting- and other foraging tracks (camera traps and records of road kills are not used as these include a different search effort). Of the 2370 records from 2008 until 2018 of wild boar in the eastern provinces of Flanders (Limburg (excluding the geographically isolated municipality of Voeren), Antwerp and Flemish Brabant), we removed 986 records which were not (yet) verified and approved by experts of Natuurpunt to increase the reliability of the observation. This resulted in 1383 wild boar occurrence recordings originating from waarnemingen.be. As a second citizen science

source of wild boar occurrences, hunting records were used. For each wild boar shot a hunting record has to be entered in the data portal of the Flemish Nature and Forestry Agency (ANB). Hunters have to provide information on body weight, sex, age class, in which game management unit the wild boar has been shot, etc. Since 2016 hunters have the possibility to enter the exact coordinates when they register hunting records. Although a large part of hunters do not record the exact coordinates, a dataset of 1510 records having exact geographic coordinates of the place where wild boar were shot was available for the period from 2016 until 2018 (Figure 1).

2.3 Environmental variables

Based on the current knowledge about wild boar habitat use and their spatial behavior in Europe, a set of nine land-use variables were selected (Table 1). The required information was retrieved from the land use map of Flanders NARA level 2 (Poelmans and Van Daele, 2014), the yearly agricultural crop maps (EPR, from 2008 until 2017 (EPR of 2018 was not yet available)) and the map of stagnant water surfaces in Flanders (including pools, puddles, ponds, fens etc. thus not including rivers, streams and canals (Packet et al., 2018)). The percentage of deciduous forest, coniferous forest, scrub and other low natural cover (natural grasslands, heathlands, wetlands, reeds), urbanised area and stagnant water in each 1 km² UTM-grid cell was calculated. Yearly agricultural crop maps were used to calculate the mean percentage of maize, the mean percentage of grasslands and the mean percentage of other crops from 2008 until 2017 in each grid cell. To assess the importance of habitat diversity, we calculated the Shannon index of habitat diversity (including deciduous forest, coniferous forest, maize, scrub and other low natural cover) per grid cell (Cornelis and Hermy, 2004). All metrics were calculated in ArcMap (ESRI, 2019).

Table 1: Nine habitat and land-use variables calculated per 1 km² UTM-grid cell within the training area (minimum convex polygon encompassing the data records, Figure 1) and in Flanders with the mean percentages of these variables in a UTM-grid cell and standard error (SE) of each variable (except for Shannon habitat diversity index which represents the mean index). Studies which report the importance of these variables in spatial use of wild boar are mentioned.

Variable	Mean ± SE training area	Mean ± SE Flanders	References
Coniferous forest	8.71% ± 0.22	3.96 % ± 0.094	Forests:
Deciduous forest	8.38 % ± 0.15	5.84 % ± 0.085	Bosch et al. (2014a), Bosch et al. (2014b), Keuling et al. (2009), Morelle et al. (2016), Thurfjell et al. (2009)
Scrub and other low natural cover	2.84 % ± 0.11	1.72 % ± 0.047	Alexander et al. (2016) & Bosch et al. (2014a)
Grasslands	14.79 % ± 0.17	17.68 % ± 0.11	Agricultural crops:

Maize	11.89 % ± 0.15	13.12 % ± 0.092	Keuling et al. (2009) & Morelle et al. (2016)
Other crops	13.70 % ± 0.24	16.83 % ± 0.15	
Urbanized area	4.97 % ± 0.11	5.08 % ± 0.063	Stillfried et al. (2017a)
Stagnant water	1.47 % ± 0.068	1.12 % ± 0.031	Ilse and Hellgren (1995)
Shannon habitat diversity index	0.71 ± 0.005	0.52 ± 0.0032	/

As Flanders has mainly a flat or gently undulating landscape, we did not include variables to characterize topography. Moreover, as Flanders is a rather small area with limited variation in weather conditions (i.e. to have an effect on wild boar), no climatic variables were included.

The degree of multicollinearity between these nine variables was calculated by computing pairwise Pearson's correlation coefficients (r-value) in R (R Development Core Team 2015) (R studio Team, 2016). The highest correlation was found to be 0.5 (between scrub and other low natural cover and other crops, supplementary materials A) which we considered not toohererr high to interfere model construction so no variables were excluded.

2.4 Species Distribution Model

As we have presence-only datasets of wild boar occurrences we opted to use MaxEnt (maximum entropy modelling) (Phillips et al., 2006) to conduct a SDM analysis. MaxEnt is a popular modelling method as it is known to produce robust models and to have a high predictive performance (Elith et al., 2006). MaxEnt models compare environmental characteristics at sites where species have been recorded with those throughout the modeled region (defined as background) (Guillera-Arroita et al., 2015; Phillips et al., 2009). MaxEnt's predictions are indices of habitat suitability (Merow et al., 2013). MaxEnt assumes all locations in the landscape to be equally likely to be sampled (Merow et al., 2013). However, due to spatially unequal sampling effort and resulting sampling bias, some environmental variables risk to be overemphasized (Kramer-Schadt et al., 2013). Both of our citizen science data sources present a different type of bias for which correction is essential.

2.4.1 Sampling bias waarnemingen.be

Given the nature of waarnemingen.be as a data portal for all species, these data gave an unique opportunity to better understand sampling bias in such data. On the basis of sightings reported, observers can be classified in groups (i.e. mammal specialists, butterfly specialist, generalists, etc.).

Not all types of observers record all species they see equally. After defining what other species an observer who submits wild boar records typically also reports, we can create a wild boar observer profile and assess sampling effort of wild boar observers throughout Flanders. A consistent wild boar observer, was defined as an observer who recorded wild boar on at least 5 separate days (see supplementary materials B for more detailed information). The sampling effort by wild boar observers is calculated as the total number of days for which mammal observations in a UTM 1x1 km grid cell are submitted (see supplementary materials B for more detailed information). This sampling effort assessment resulted in a raster file that can be used in a MaxEnt model to select background data corrected for sampling bias: background data are selected with a higher probability in areas with higher sampling effort than in areas with lower sampling effort.

2.4.2 Sampling bias hunting bag

Wild boar hunting in Flanders is only allowed on those properties for which the hunter has the hunting rights – so called hunting grounds. Outside these hunting grounds, there is no hunting so no wild boar shot can be reported, this results in areas without sampling effort. A map of hunting grounds is therefore used to construct a raster file based on the percentage of hunted area in each 1x1 km UTM grid cell. This raster is used in MaxEnt to select background data corrected for sampling bias: background data are selected with a higher probability in grid cells with a high percentage of the area being hunted.

2.4.3 Spatial thinning

To assess if defining sampling effort using observers' characteristics of waarnemingen.be or using hunting ground information is a good method to correct for sampling bias, we compared the results of these approaches with those of spatial thinning or filtering. This method is often used to handle sampling bias (Kramer-Schadt et al., 2013; Swinnen et al., 2017). Applying spatial thinning, environmental variables do not risk to be overemphasized. This over-representation is possible when recorded species occurrences are spatially clumped resulting in spatial autocorrelation (Kramer-Schadt et al., 2013). Spatial thinning is applied by removing data from waarnemingen.be or hunting bag data closer than the minimum "nearest neighbor index distance". The latter is the ratio between the observed distance and the expected distance, being the average distance between neighbors whenever the observation would be random distributed thus not spatially autocorrelated). Using the *spThin* R package (version 0.1.0, Aiello-Lammens et al., 2015), this nearest index distance was found to be 0.23 km for the waarnemingen.be dataset and 0.22 km for the hunting bag dataset. Applying spatial thinning resulted in a thinned dataset of 627 occurrences of waarnemingen.be and 729 occurrences based on hunting bag records. Background data selection based on this spatial thinned dataset happened at random.

2.4.4 MaxEnt

All background data were selected within the minimum convex polygon (MCP) encompassing all data. The resulting MCP used as training area encompassed 4940 km² (Table 1 & Figure 1). Different MaxEnt models were constructed (Figure 2). The first two MaxEnt models were based on waarnemingen.be data and background data selection for these models was done taking the sampling bias grid based on these data into account. A first model was constructed using the full dataset and validated using hunting bag dataset. A second model was constructed using a random selection of 70% of the waarnemingen.be dataset and validated using the remaining 30%. Similarly, two MaxEnt models based on hunting bag data, and its corresponding sampling bias file for background selection, were built: a first model was constructed using the full hunting bag dataset and validated using the waarneming.be data and a second model was constructed using a random selection of 70% of the hunting bag dataset and validated using the remaining 30%. Using this same methodology, 4 MaxEnt models were constructed based on the spatially thinned datasets of or waarnemingen.be or hunting bag. For these 4 models, background data are randomly selected (Figure 2).

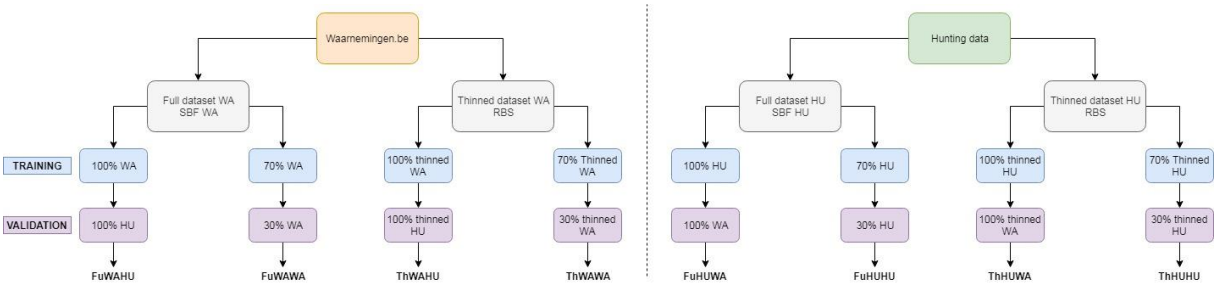

Figure 2: MaxEnt models, datasets, training and validation data selection and background selection with WA being data from waarnemingen.be, HU being data from hunting bag, Fu being the full dataset of either WA or HU, Th being the thinned dataset of either WA or HU, SBF being sampling bias file for background selection and RBS being random background selection.

Before running the MaxEnt models, the optimal settings were defined using the *ENMeval* R package (version 0.3.0, Muscarella et al., 2014). In this *ENMeval* R package, different methods are provided for partitioning training data. Our goal is to conduct predictions for the whole of Flanders, thus involving model transfer across space. We therefore used the block separation method for partitioning training data as this method was found suitable for studies involving model transfer across space (Muscarella et al., 2014). The block method partitions training data according to latitude and longitude into 4 geographically separated parts. We tested a range of different settings and their combinations using random background selection (1500 points). A regularization multiplier varying from 0.5 to 4, using 0.5 step intervals (higher values result in stronger smoothing and less complex models) and feature classes varying between linear (L), quadratic (Q) and product (P) or a combination of these

classes (more classes enable more flexible and complex fits to the observed data) (Muscarella et al., 2014). Model performances of all possible setting combinations were compared using the AUC-value (area under the receiver-operating characteristics curve or ROC-curve). The settings of the models with highest AUC-value were considered optimal settings and were further used in the final MaxEnt models. With optimal settings, all models (Figure 2) were fitted using MaxEnt version 3.3.3 in the *dismo* R package (version 1.1-4, Hijmans et al., 2017). Following the method of Marchi and Ducci (2018) to evaluate the robustness of each variable delivered by a model, each model was ran 50 times, each times randomly splitting the datasets into 70% training and 30% validation (for the models using this approach, models using the full dataset have the same full dataset over the 50 runs) and for each run 1500 background points were selected based on the sampling bias files or at random. Model performance was analyzed using the AUC-values averaged over the 50 runs. Based on each of these models, habitat suitability projections were made for the rest of Flanders and are then averaged over the 50 runs. The correlations between different model predictions are tested using the Pearson correlation *layerStat* function of the *raster* R package (version 2.8-19, Hijmans et al., 2019). Combining all 8 MaxEnt models, the average, minimum and maximum possible habitat suitability was calculated. The mean variable importance over all eight models are calculated.

Extrapolation outside the training range of a SDM can result in less reliable predictions (Fitzpatrick and Hargrove, 2009). To get an idea of the uncertainty of extrapolation outside the training area, the extent of environmental differences between model training and projection area can be calculated using multivariate environmental similarity surface (MESS) maps. MESS-analysis measures the similarity between the dataset used to train the model and the newly projected areas on variable at a time (degree of extrapolation of univariate ranges for individual variables). However, these MESS-maps do not visualize multivariate combinations of environmental conditions which are not represented in the dataset. We therefore used the proposed method of Zurell et al. (2012) to determine environmental overlap as an extended MESS-analysis. By determining environmental overlap, parts of the environmental range of variables in Flanders which are within the sampled, univariate range of individual variables of the training set but which represent new multivariate combinations are identified. This is done by splitting training data into a 3 bins in which each bin holds a unique combination of environmental predictor values. Bins in the predictions dataset that do not overlap with training bins are defined as novel environments in which model extrapolation occurs (Zurell et al., 2012).

3. Results

For all models, optimal settings were found to be a regularization multiplier of 0.5 and feature classes LQP. Model performances (defined by averaged AUC-values) of all models ranged between 0.78 and 0.88 (Table 2). The highest AUC values were found when trained and validated set had the same

source of species occurrences. Small standard deviations reflect highly robust variables used for the Maxent models.

The percentage of coniferous forest is the most important variable defining habitat suitability over all models (Table 2). Furthermore, deciduous forest, scrub and other low natural cover, water and maize showed intermediate importance. The remaining variables only resulted in a minor contribution to habitat suitability. With increasing percentages of both forest types and scrub and other low natural cover, habitat suitability increases (supplementary materials C).

Table 2: Variable importance of all variables in MaxEnt models together with AUC-values as a measure of model performances. These variable importances are averaged (including standard deviation) over the 50 model runs for each of the eight models. Variable importances are scaled to the AUC-value (the sum of all values equals the AUC-value, not 100%). The last column present the mean over all models with the combined standard deviation

	Waarnemingen.be				**Hunting bag**				
Dataset	Full		Thinned		Full		Thinned		
Training-validations	WA-HU	70-30 WA	WA-HU	70-30 WA	HU-WA	70-30 HU	HU-WA	70-30 HU	MEAN
Model name	FuWAHU	FuWAWA	ThWAHU	ThWAWA	FuHUWA	FuHUHU	ThHUWA	ThHUHU	
AUC	0.74 ± 0.01	0.84 ± 0.01	0.79 ± 0.01	0.86 ± 0.01	0.84 ± 0.01	0.86 ± 0.01	0.81 ± 0.01	0.84 ±0.13	
				Variable importance (%)					
Coniferous forest	28.01 ± 1.41	29.00 ± 3.02	23.35 ± 1.88	22.44 ± 2.96	50.43 ± 2.01	50.53 ± 2.22	49.87 ± 1.51	51.50 ± 2.04	38.14 ± 12.81
Deciduous forest	13.93 ± 1.53	16.47 ± 2.92	18.69 ± 2.15	20.65 ± 3.66	4.32 ± 0.97	4.65 ± 0.89	4.66 ± 0.66	4.82 ± 1.14	11.02 ± 6.95
Maize cover	11.47 ± 0.89	13.78 ± 2.13	13.21 ± 1.55	16.15 ± 2.72	6.7 ± 1.75	7.47 ± 1.86	4.05 ± 0.75	4.25 ± 0.97	9.63 ± 4.64
Scrub and other low natural cover	3.07 ± 0.64	3.96 ± 1.48	5.11 ± 1.28	5.74 ± 2.16	10.26 ± 0.83	8.91 ± 1.51	9.74 ± 0.88	9.62 ± 1.59	7.06 ± 3.04
Stagnant water	7.08 ± 0.84	9.26 ± 1.94	8.17 ± 1.60	9.28 ± 2.29	2.00 ± 0.50	2.35 ± 0.62	1.76 ± 0.50	2.13 ± 0.62	5.25 ± 3.51
Other crops	1.61 ± 0.38	2.23 ± 0.82	2.00 ± 0.43	2.29 ± 0.76	3.83 ± 0.71	4.39 ± 1.16	4.41 ± 0.78	4.72 ± 1.02	3.19 ± 1.43
Shannon-Index	2.31 ± 1.23	2.52 ± 1.45	3.19 ± 1.52	3.63 ± 1.73	3.23 ± 1.26	3.92 ± 1.37	3.28 ± 0.88	3.11 ± 1.13	3.15 ± 1.42
Urban cover	4.35 ± 0.52	4.26 ± 1.34	3.68 ± 0.67	3.98 ± 1.14	2.04 ± 0.54	2.28 ± 0.70	1.78 ± 0.36	2.02 ± 0.68	3.05 ± 1.31
Grassland cover	2.17 ± 0.39	2.53 ± 0.69	1.61 ± 0.58	1.86 ± 0.70	1.17 ± 0.39	1.49 ± 0.44	1.44 ± 0.35	1.83 ± 0.60	1.76 ± 0.67

High Pearson correlation coefficients between prediction maps reflect the high similarity between predicted habitat suitability based on the different models (Table 3, supplementary materials D). The averaged habitat suitability over all eight models shows that highest suitable areas were found in the East of Flanders (Figure 3). Towards the West of Flanders, the overall habitat suitability was found to be lower (Figure 3). However, small patches of highly suitable habitat distributed in a matrix of less suitable habitat are found all over the region and occur in high numbers in the centre of Flanders. Based on the averaged habitat suitability over all eight models, although of the total area, 3.75 % is currently occupied (based on all waarnemingen.be and hunting bag occurrences), a remaining 8.37% of suitable habitat (habitat suitability > 0.5) is not yet occupied (Table 4). Of the total area, suitable habitat (habitat suitability > 0.5) raises from 7.67 % to 19.21 % when minimum and maximum habitat suitability are compared (supplementary materials E).

Our environmental overlap MESS-analysis showed that model projections towards the rest of Flanders involved predictions towards novel environments in the West and South-East of Flanders (supplementary materials F) indicating extrapolation of our models in these areas.

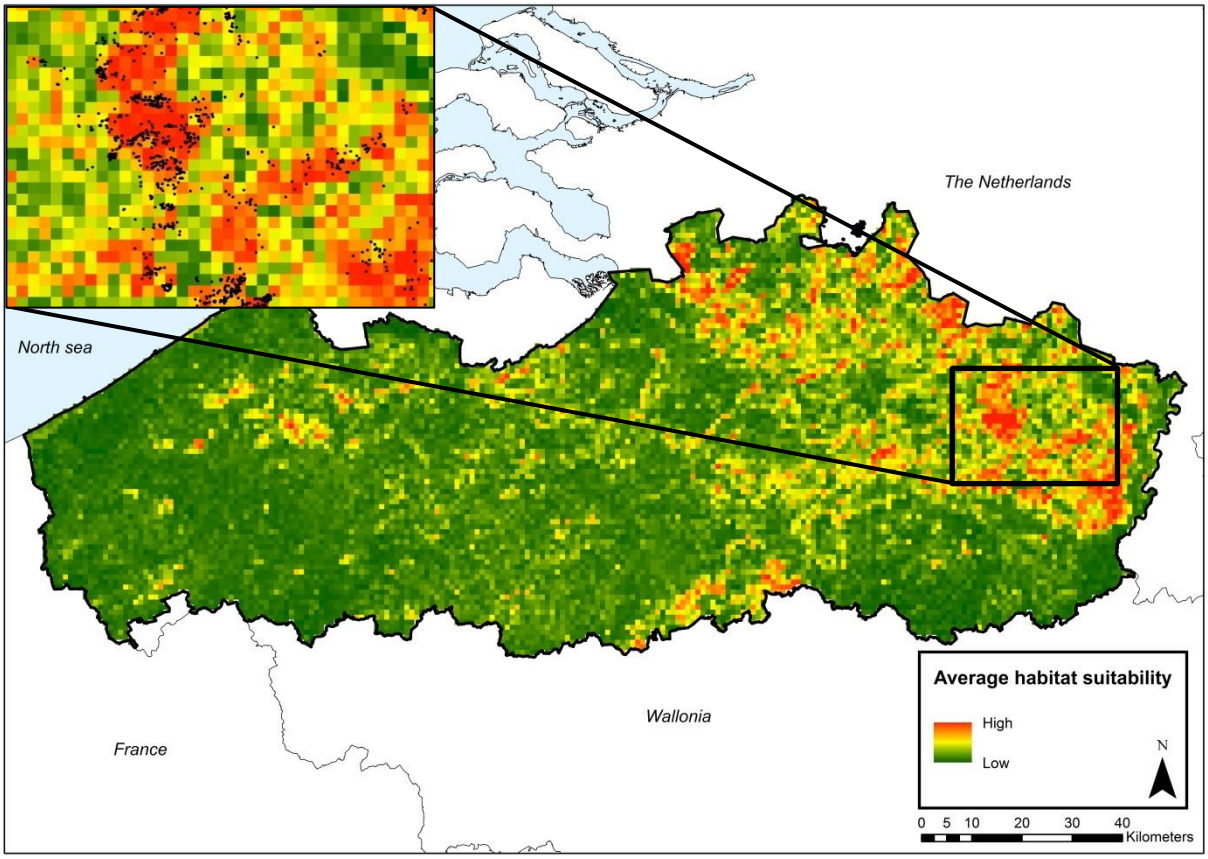

Figure 3: MaxEnt prediction of habitat suitability for wild boar in Flanders averaged over all eight models. Red colors indicate high habitat suitability, green colors indicate low habitat suitability. Dots are waarnemingen.be and hunting bag occurrences. Model predictions of all separate models can be found in supplementary materials D.

Table 3: Pearson correlations between model predictions.

	FuHUHU	FuHUWA	FuWAHU	FuWAWA	ThHUHU	ThHUWA	ThWAHU	ThWAWA
FuHUHU	1.00							
FuHUWA	1.00	1.00						
FuWAHU	0.98	0.98	1.00					
FuWAWA	0.98	0.98	1.00	1.00				
ThHUHU	1.00	1.00	0.98	0.98	1.00			
ThHUWA	0.80	0.80	0.76	0.74	0.80	1.00		
ThWAHU	0.84	0.84	0.80	0.78	0.84	0.98	1.00	
ThWAWA	0.83	0.83	0.80	0.78	0.83	0.98	1.00	1.00

Table 4: Occupied versus unoccupied suitable habitat (defined as habitat suitability > 0.5) in Flanders based on the averaged habitat suitability over all eight models. Percentages are defined as the percentage of grid cells being occupied or unoccupied by all waarnemingen.be and hunting bag occurrences.

	Percentage in Flanders
Suitable area	12.14 %
Occupied area	3.75 %
Unoccupied suitable area	8.37 %

4. Discussion

By relating wild boar occurrences to environmental variables, we obtained a better understanding of factors influencing habitat suitability for wild boar in the highly anthropogenic landscape of Flanders.. Based on our model projections, remaining suitable habitat was mainly found in the East of Flanders adjacent to the current distribution area and in some areas in the centre of Flanders. Towards the West of the region only a limited amount of suitable habitat was found.

Forest played an important role in defining habitat suitability. This is in line with previous studies who found that forest plays a key role in landscape use and range expansion (Alexander et al., 2016; Morelle et al., 2016; Rutten et al., 2019). Coniferous forest was found more important than deciduous forest in defining habitat suitability. While some studies did not consider separate forest types having a different contribution (i.e. they did not differentiate between different forest types) (Alexander et al., 2016; Bosch et al., 2014b), Thurfjell et al. (2009) in Sweden and Fonseca (2008) in Poland reported deciduous forest more preferred compared to coniferous forest. A potential reason mentioned by

Thurfjell et al. (2009) and Fonseca (2008) is the high presence of food resources in deciduous forest through mast. These findings are in contrast to ours. A potential explanation may be that intensive agricultural systems like the one in Flanders (also found in the Netherlands, Denmark, parts of Germany, France etc.) provide a surfeit of food outside forests leading wild boar populations to be less dependent on mast in deciduous forest. Although scrub and low cover is generally considered not improving habitat suitability due to limited shelter opportunities (Alexander et al., 2016; Bosch et al., 2014a), a considerable contribution of this landscape type to habitat suitability was found. A possible explanation may be that this is an adaptation due to limited and fragmented forest availability: while scrub and low cover areas are often considered as marginal habitats, we think that wild boar can find sufficient shelter in this vegetation allowing them to move through a highly anthropogenic landscape. Moreover, providing shelter in forests might be determined specifically by undergrowth in forests: open forests provide less shelter then forests with scrub-like undergrowth. However, as there were no available maps on undergrowth cover in forests, this could not be assessed. The relationship of both the percentage of maize and water with habitat suitability was found not to be uniform between models based on waarnemingen.be data and hunting bag data. However, high correlations between habitat suitability projections of all eight models were found illustrating the overall consistency of our results.

The Flemish landscape is characterized by a much higher anthropogenic pressure then study areas of previous conducted studies which allowed us to assess if there are limits to the flexibility of wild boar towards habitat use. Urban cover did not have a large negative impact on habitat suitability. It has been shown that wild boar show substantial behavioural plasticity to adjust to human-dominated environments i.e. landscape of fear (Stillfried et al., 2017a): wild boar tolerate human presence by modulating their risk perception indicated by lower flee distances of urban boars versus rural boars, adjust their spatial use (use of recreational forest with high human presences) and even use human-associated habitat classes by modulating the perception of harmless anthropogenic risk. Habitat diversity was found not important confirming adaptive and highly flexible habitat utilization by wild boar in response to anthropogenic disturbances (Calenge et al., 2002; Keuling et al., 2008; Maillard and Fournier, 2014). These results show that we have not yet reached the limits of wild boar being able to use human-dominated habitat types or habitat like scrub and other low natural cover which are generally not considered to improve habitat suitability when adjusting to anthropogenic landscapes. We therefore acknowledge that given the high behavioural plasticity of wild boar in adjusting towards human-dominated areas, wild boar might be able to further adjust to less suitable areas, to changing environments and changing climate (Lowry et al., 2013). MESS maps showed extrapolation to novel environments in the East of Flanders where the landscape is dominated by agriculture and there are limited areas covered by forests. If wild boar can further adjust to these open novel environments, it is possible that areas which are currently considered not suitable may still become colonised.

Current model projections showed the existence of yet still unoccupied highly suitable habitat, although generally scattered throughout the landscape, in the East and parts of the centre of Flanders. On the other hand, the currently unoccupied habitats in the West are less suitable for wild boar. Although population numbers and distribution range expanded fast since their recolonisation in 2006 (Scheppers et al. 2014), based on the models one would expect limited future expansion of the current wild boar distribution range in Flanders as only 12.14% of the Flemish landscape exists out of suitable habitat. However, since currently only 3.75% of Flanders is occupied, only one third of the suitable habitat is currently used so the current expansion range can still triple in area.

To study large-scale patterns, a large amount of data needs to be collected (Bonney et al., 2009). Using citizen science of waarnemingen.be we did not only have a large amount of wild boar occurrence data, but also information on search effort derived from other wildlife observations. This allowed to define sampling effort in a new way to create bias files for background selection. However, we want to acknowledge that differences in detection probabilities of different kind of occurrence data (sightings, footprints etc.) were not quantified and thus not assessed if this affected modelling results as this was outside the scope of this study. Furthermore, by using information on hunting grounds we could correct for sampling bias in the models based on citizen science data originating from hunting bag information. By comparing these new methods to the already used method of spatial thinning, we found very similar outcomes with comparable model performances. Analysing observers' characteristics based on their observation recorded in waarnemingen.be has previously been found useful when calculating search effort corrected population trends in butterflies and birds (Herremans, 2010). Although spatial thinning involves less effort than defining sampling bias, spatial thinning reduces the amount of data which can be problematic for small datasets for example of species with a low detection probability or datasets of rare species. In these cases, creating bias files using our presented method can offer a solution. Moreover, as hunting bag data was found to be an important source for large-scale SDM for wild boar in Europe, given the fact that they are the most available and standardized source of wild boar occurrences throughout Europe (ENETwild consortium et al., 2019), correcting sampling bias based on using hunting ground information can be useful and easily applicable, also on larger scales.

5. Conclusion

Wild boar is expected to expand its distribution range in Flanders. As HWI in an anthropogenic landscape such as Flanders strongly affects stakeholder acceptance of wild boar, being able to conduct risk assessments linked to the future wild boar dispersal is essential to assess the future possible evolution of HWI. A risk assessment allows to prioritize management actions in areas where wild boar is expected due to high habitat suitability. Moreover, crop damage is one of the HWI raising most concerns because of the high economic impact (Carnis and Facchini, 2012; Schley et al., 2008).

Recent research of Rutten et al. b (not in press) assessed landscape factors influencing crop damage probability in Flanders. However, since these damage probability predictions did not yet include future distribution of wild boar, creating this SDM of wild boar in Flanders is an essential step to predict the geographic distribution and extent of damage risks linked to further wild boar dispersal. Using the combined information on habitat suitability and damage probability within areas occupied by wild boar, implementing preventive measures where the highest damage risks are localised, can allow to decrease crop damage and thus increasing stakeholder acceptance. Furthermore, recent outbreaks of African Swine Fever (ASF) in several eastern European countries including an outbreak in Wallonia in September 2018 raises concerns due to major economic impacts (Costard et al., 2009; Lange et al., 2018). The gained understanding on the future expected distribution of wild boar in Flanders will be essential towards a risk assessment with potential future ASF outbreaks.

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7. References

Acevedo, P., Vicente, J., Höfle, U., Cassenello, J., Ruiz-Fons, F., Gortazar, C., 2007. Estimation of European wild boar relative abundance and aggregation: a novel method in epidemiological risk assessment. Epidemiology and Infections 135, 519-527.

Aiello-Lammens, M.E., Boria, R.A., Radosavljevic, A., Vilela, B., Anderson, R.P., 2015. Package ‘spThin’: Functions for Spatial Thinning of Species Occurrence Records for Use in Ecological Models.

Alexander, N., Massei, G., Wint, W., 2016. The European distribution of Sus scrofa. Model outputs from the project described within the poster–where are all the boars? An attempt to gain a continental perspective. Open Health Data 4.

Araujo, M.B., Guisan, A., 2006. Five (or so) challenges for species distribution modelling. Journal of biogeography 33, 1677-1688.

Baldwin, R., 2009. Use of maximum entropy modeling in wildlife research. Entropy 11, 854-866.

Barua, M., Bhagwas, S.A., Jadhav, S., 2013. The hidden dimensions of human–wildlife conflict: Health impacts, opportunity and transaction costs. Biological Conservation 157.

Bellamy, C., Scott, C., Altringham, J., 2013. Multiscale, presence-only habitat suitability models: fine-resolution maps for eight bat species. Journal of Applied Ecology 50, 892-901.

Bieber, C., Ruf, T., 2005. Population dynamics in wild boar Sus scrofa: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. Journal of Applied Ecology 42, 1203-1213.

Bonney, R., Cooper, C.B., Dickinson, J., Kelling, S., Phillips, T., Rosenberg, K.V., Shirk, J., 2009. Citizen science: a developing tool for expanding science knowledge and scientific literacy. BioScience 59, 977-984.

Boria, R.A., Olson, L.E., Goodman, S.M., Anderson, R.P., 2014. Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. Ecological Modelling 275, 73-77.

Bosch, J., De La Torre, A., Alexandrov, T., Iglesias, I., Miteva, A., Muñoz, M.J., 2014a. Can habitat suitability predict the presence of wild boar? Suitable land uses vs. georeferenced data in Bulgaria. Folia Zoologica 63, 194-206.

Bosch, J., Mardones, F., Pérez, A., De la Torre, A., Muñoz, M.J., 2014b. A maximum entropy model for predicting wild boar distribution in Spain. Spanish Journal of Agricultural Research 12, 984-999.

Bradley, B.A., Wilcove, D.S., Oppenheimer, M., 2010. Climate change increases risk of plant invasion in the Eastern United States. Biological Invasions 12, 1855-1872.

Cahill, S., Llimona, F., Cabañeros, L., Calomardo, F., 2012. Habituation of wild boar (Sus scrofa) to urban areas: traits from Collserola Natural Park (Barcelona) and comparison with other cities. Animal Biodiversity and Conservation 35, 221-233.

Calenge, C., Maillard, D., Vassant, J., Brandt, S., 2002. Summer and hunting season home ranges of wild boar (Sus scrofa) in two habitats in France. Game and Wildlife Science (France).

Carnis, L., Facchini, F., 2012. Une approche économique des dégâts de gibier. Indemnisation, prix et propriété. économie rurale Janvrier-Mars, 126 - 142.

Carpenter, L., Decker, D., Lipscomb, J.F., 2013. Stakeholder Acceptance Capacity in Wildlife management. Human Dimensions of Wildlife: An International Journal 5, 5-19.

Červinka, J., Riegert, J., Grill, S., Šálek, M., 2015. Large-scale evaluation of carnivore road mortality: the effect of landscape and local scale characteristics. Mammal Research 60, 233-243.

Cornelis, J., Hermy, M., 2004. Biodiversity relationships in urban and suburban parks in Flanders. Landscape and Urban Planning 69, 385-401.

Costard, S., Wieland, B., De Glanville, W., Jori, F., Rowlands, R., Vosloo, W., Roger, F., Pfeiffer, D.U., Dixon, L.K., 2009. African swine fever: how can global spread be prevented? Philosophical Transactions of the Royal Society B: Biological Sciences 364, 2683-2696.

Crall, A.W., Jarnevich, C.S., Young, N.E., Panke, B.J., Renz, M., Stohlgren, T.J., 2015. Citizen science contributes to our knowledge of invasive plant species distributions. Biological invasions 17, 2415-2427.

Dellicour, S., Prunier, J.G., Piry, S., Eloy, M.-C., Bertouille, S., Licoppe, A., Frantz, A.C., Flamand, M.-C., 2019. Landscape genetic analyses of Cervus elaphus and Sus scrofa: comparative study and analytical developments. Heredity, 1.

Demolder, H., Schneiders, A., Spanhove, T., Maes, D., Van Landuyt, W., Adriaens, T., 2014. Natuurrapport - Toestand en trend van ecosystemen en ecosysteemdiensten in Vlaanderen. Hoofdstuk 4: Toestand biodiversiteit. 0-83.

Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29, 129-151.

Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. Annual review of ecology, evolution, and systematics 40, 677-697.

ENETconsortium, Croft, S., Smith, G., Acevedo, P., Vicente, J., 2019. Wild boar in focus: initial model outputs of wild boar distribution based on occurrence data and identification of priority areas for data collection. EFSA supporting publication 2019 EN-1533, 26.

Faunafonds, 2014. Jaarverslag Faunafonds: 2014. 4-54.

Fischer, M.L., Sullivan, M.J.P., Greiser, G., Guerro-Cascado, J., Heddergott, M., Hohmann, U., Keuling, O., Lang, J., Martin, I., Michler, F.-U., Winter, A., Klein, R., 2015. Assessing and predicting the spread of non-native raccoons in Germany using hunting bag data and dispersal weighted models. Biological Invasions.

Fitzpatrick, M.C., Hargrove, W.W., 2009. The projection of species distribution models and the problem of non-analog climate. Biodiversity and Conservation 18, 2255.

FOD Economie., 2011. Bevolking van Belgische Nationaliteit volgens Administratieve Eenheden.

Fonseca, C., 2008. Winter habitat selection by wild boar Sus scrofa in southeastern Poland. European Journal of Wildlife Research 54, 361.

Guillera-Arroita, G., Lahoz-Monfort, J.J., Elith, J., Gordon, A., Kujala, H., Lentini, P.E., McCarthy, M.A., Tingley, R., Wintle, B.A., 2015. Is my species distribution model fit for purpose? Matching data and models to applications. Global Ecology and Biogeography 24, 276-292.

Herremans, M., 2010. Monitoren via waarnemingen.be. Natuur oriolus 76, 94-108.

Herremans, M., Gielen, K., 2013. Was 2013 een super vlinderjaar? Cijfers uit losse waarnemingen 2009-2013, in: Natuurpunt (Ed.). Natuurpunt.focus.

Hijmans, R., van Etten, J., Sumner, M., Cheng, J., Bevan, A., Bivand, R., Busetto, L., Canty, M., Forrest, D., Ghosh, A., Golicher, D., Gray, J., Greenberg, J., Hiemstra, P., Karney, C., Mattiuzzi, M., Mosher, S., Nowosad, J., Pebesma, E., Lamigueiro, O.P., Racine, E.B., Rowlingson, B., Shortridge, A., Venables, B., Wueest, R., 2019. Package 'raster': geographic data analysis and modeling.

Hijmans, R.J., Phillips, S., Leathwick, J., Elith, J., 2017. Package 'dismo'.

Ilse, L.M., Hellgren, E.C., 1995. Resource partitioning in sympatric populations of collared peccaries and feral hogs in southern Texas. Journal of Mammalogy 76, 784-799.

Keuling, O., Podgórski, T., Monaco, A., Melletti, M., Merta, D., Albrycht, M., Genov, P.V., Gethöffer, F., Vetter, S.G., Jori, F., Scalera, R., Gongora, J., 2018. Eurasian Wild Boar Sus scrofa (Linnaeus, 1758), in: Melletti, M., Meijaard, E. (Eds.), Ecology, Conservation and Management of Wild Pigs and Peccaries. Cambridge University Press, Cambridge, UK, pp. 202-234.

Keuling, O., Stier, N., Roth, M., 2008. How does hunting influence activity and spatial usage in wild boar Sus scrofa L.? european Journal of Wildlife research 54, 729.

Keuling, O., Stier, N., Roth, M., 2009. Commuting, shifting or remaining?: Different spatial utilisation patterns of wild boar Sus scrofa L. in forest and field crops during summer. Mammalian Biology 74, 145-152.

Khanum, R., Mumtaz, A., Kumar, S., 2013. Predicting impacts of climate change on medicinal asclepiads of Pakistan using Maxent modeling. Acta Oecologica 49, 23-31.

Kotulski, Y., König, A., 2008. Conflicts, Crises and Challenges: Wild Boar in the Berlin City - a Social Empirical and Statistical Survey. Natura Croatica 17, 233-246.

Kozak, K.H., Graham, C.H., Wiens, J.J., 2008. Integrating GIS-based environmental data into evolutionary biology. Trends in ecology & evolution 23, 141-148.

Kramer-Schadt, S., Niedballa, J., Pilgrim, J.D., Schröder, B., Lindenborn, J., Reinfelder, V., Stillfried, M., Heckmann, I., Scharf, A.K., Augeri, D.M., 2013. The importance of correcting for sampling bias in MaxEnt species distribution models. Diversity and Distributions 19, 1366-1379.

Lange, M., Guberti, V., Thulke, H.H., 2018. Understanding ASF spread and emergency control concepts in wild boar populations using individual-based modelling and spatio-temporal surveillance data. EFSA Supporting Publications 15, 1521.

Linell, J.D.C., Swenson, J.E., Andersen, R., 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. Animal Conservation 4, 345-349.

Lowry, H., Lill, A., Wong, B.B., 2013. Behavioural responses of wildlife to urban environments. Biological reviews 88, 537-549.

Maillard, D., Fournier, P., 2014. Effects of shooting with hounds on size of resting range of wild boar (Sus scrofa L.) groups in Mediterranean habitat. Journal of Mountain Ecology 3.

Mair, L., Harrison, P.J., Jönsson, M., Löbel, S., Nordén, J., Siitonen, J., Lämås, T., Lundström, A., Snäll, T., 2017. Evaluating citizen science data for forecasting species responses to national forest management. Ecology and evolution 7, 368-378.

Marchi, M., Ducci, F., 2018. Some refinements on species distribution models using tree-level National Forest Inventories for supporting forest management and marginal forest population detection. iForest-Biogeosciences and Forestry 11, 291.

Massei, G., Kindberg, J., Licoppe, A., Gacic, D., Sprem, N., Kamler, J., Baubet, E., Hohmann, U., Monaco, A., Ozolins, J., Cellina, S., Podgorski, T., Fonseca, C., Markov, G., Pokorny, B., Rosell, C., Nahlik, A., 2015. Wild boar populations up, numbers of hunters down? A review of trends and implications for Europe. Pest Management Science 71, 492-500.

Mayer, J.J., 2018. Introduced Wild Pigs in North America: History, Problems and Management, in: Melletti, M., Meijaard, E. (Eds.), Ecology, Conservation and Management of Wild Pigs and Peccaries. Cambridge University Press.

Merow, C., Smith, M.J., Silander Jr, J.A., 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography 36, 1058-1069.

Messmer, T.A., 2000. The emergence of human±wildlife con¯ict management: turning challenges into opportunities. International Biodeterioration & Biodegradation 45, 97-102.

Metzger, M.J., Bunce, R.G., Jongman, R.H., Sayre, R., Trabucco, A., Zomer, R., 2013. A high-resolution bioclimate map of the world: a unifying framework for global biodiversity research and monitoring. Global Ecology and Biogeography 22, 630-638.

Morelle, K., Fattebert, J., Mengal, C., Lejeune, P., 2016. Invading or recolonizing? Patterns and drivers of wild boar population expansion into Belgian agroecosystems. Agriculture Ecosystems & Environment 222, 267-275.

Muscarella, R., Galante, P.J., Soley-Guardia, M., Boria, R.A., Kass, J.M., Uriarte, M., Anderson, R.P., 2014. ENM eval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. Methods in Ecology and Evolution 5, 1198-1205.

Packet, J., Scheers, K., Smeekens, V., Leyssen, A., Wils, C., Denys, L., 2018. Watervlakken versie 1.0: polygonenkaart van stilstaand water in Vlaanderen. Een nieuw instrument voor onderzoek, water-, milieu- en natuurbeleid. Rapporten van het Instituut voor Natuur- en Bosonderzoek.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecological modelling 190, 231-259.

Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecological applications 19, 181-197.

Podgórski, T., Baś, G., Jędrzejewska, B., Sönnichsen, L., Śnieżko, S., Jędrzejewski, W., Okarma, H., 2013. Spatiotemporal behavioral plasticity of wild boar (Sus scrofa) under contrasting conditions of human pressure: primeval forest and metropolitan area. Journal of Mammalogy 94, 109-119.

Poelmans, L., Van Daele, T., 2014. Landgebruikskaart NARA-T 2014.

R Development Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Redpath, S.M., Young, J., Evely, A., Adams, W.M., Sutherland, W.J., Whitehouse, A., Amar, A., Lambert, R.A., Linnell, J.D., Watt, A., 2013. Understanding and managing conservation conflicts. Trends in ecology & evolution 28, 100-109.

Rutten, A., Casaer, J., Vogels, M.F., Addink, E.A., Vanden Borre, J., Leirs, H., 2018. Assessing agricultural damage by wild boar using drones. Wildlife Society Bulletin 42, 568-576.

Rutten, A., Cox, K., Scheppers, T., Vanden Broecke, B., Leirs, H., Casaer, J., 2019. Analysing the recolonisation of a highly fragmented landscape by wild boar using a landscape genetic approach. Wildlife Biology 1, 1-11

Saez-Royuela, C., Telleria, J.L., 1986. The increased population of th Wild Boar (Sus scrofa L.) in Europe. Mammal Review 16, 97-101.

Saito, M., Koike, F., Momose, H., Mihira, T., Uematse, S., Othani, T., Sekiyama, K., 2012. Forecasting the range expansion of a recolonising wild boar Sus scrofa population. Wildlife Biology 18, 383-392.

Scheppers, T., Huysentruyt, F., Neukermans, A., Verschaffel, E., Casaer, J., 2014. Grofwildjacht in Vlaanderen - Cijfers En Statistieken 2013. INBO rapport, 1-93.

Schley, L., Dufrêne, M., Krier, A., Frantz, A.C., 2008. Patterns of crop damage by wild boar (Sus scrofa) in Luxembourg over a 10-year period. European Journal of Wildlife Research 54, 589-599.

Sillero, N., 2011. What does ecological modelling model? A proposed classification of ecological niche models based on their underlying methods. Ecological Modelling 222, 1343-1346.

Steeman, R., Vanreusel, W., Barendse, R., Verloove, F., Wysmantel, N., Van den Bussche, W., Gyselinck, T., Hendrickx, P., Zwaenepoel, A., Van Vooren, P., 2017. Waarnemingen. be–Plant occurrences in Flanders and the Brussels Capital Region, Belgium. PhytoKeys, 1.

Stillfried, M., Gras, P., Börner, K., Göritz, F., Painer, J., Röllig, K., Wenzler, M., Hofer, H., Ortmann, S., Kramer-Schadt, S., 2017a. Secrets of Success in a Landscape of Fear: Urban Wild Boar Adjust Risk Perception and Tolerate Disturbance. Frontiers in Ecology and Evolution 5, 1-12.

Stillfried, M., Gras, P., Busch, M., Börner, K., Kramer-Schadt, S., Ortmann, S., 2017b. Wild inside: Urban wild boar select natural, not anthropogenic food resources. PloS one 12, e0175127.

Swinnen, K., Vercayie, D., Vanreusel, W., Barendse, R., Boers, K., Bogaert, J., Dekeukeleire, D., Driessens, G., Dupriez, P., Jooris, R., 2018. Waarnemingen. be–Non-native plant and animal occurrences in Flanders and the Brussels Capital Region, Belgium. BioInvasions Records 7, 335-342.

Swinnen, K.R., Strubbe, D., Matthysen, E., Leirs, H., 2017. Reintroduced Eurasian beavers (Castor fiber): colonization and range expansion across human-dominated landscapes. Biodiversity and Conservation 26, 1863-1876.

Thurfjell, H., Ball, J.P., Ahlén, P.-A., Kornacher, P., Dettki, H., Sjöberg, K., 2009. Habitat use and spatial patterns of wild boar Sus scrofa (L.): agricultural fields and edges. European Journal of Wildlife Research 55, 517-523.

Treves, A., Wallace, R.B., Naughton-Treves, L., Morales, A., 2006. Co-Managing Human–Wildlife Conflicts: A Review. Human Dimensions of Wildlife 11, 383-396.

Vercayie, D., Herremans, M., 2015. Citizen science and smartphones take roadkill monitoring to the next level. Nature Conservation 11, 29.

Warren, D.L., Wright, A.N., Seifert, S.N., Shaffer, H.B., 2014. Incorporating model complexity and spatial sampling bias into ecological niche models of climate change risks faced by 90 C alifornia vertebrate species of concern. Diversity and distributions 20, 334-343.

Zurell, D., Elith, J., Schröder, B., 2012. Predicting to new environments: tools for visualizing model behaviour and impacts on mapped distributions. Diversity and Distributions 18, 628-634.