Spatial epidemiology of African swine fever: Host, landscape and anthropogenic drivers of disease occurrence in wild boar

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ABSTRACT

Host abundance and landscape structure often interact to shape spatial patterns of many wildlife diseases. Emergence, spread, and persistence of African swine fever (ASF) among wild boar in eastern Europe has raised questions on the factors underlying ASF dynamics in this novel host-pathogen system. This work identifies drivers of ASF occurrence in natural wild boar population. We evaluated factors shaping the probability of ASF-postitive wild boar during the first three years (2014-2016) of the ASF epidemic in Poland. We expected to observe positive effects of wild boar density, proportion of forested area, human activity, and proximity to previous infections on ASF case probability. We tested these predictions using the infection status of 830 wild boar samples and generalized mixed-effects models. The probability of ASF case increased from 3 to 20% as population density rose from 0.4 to 2 ind./km^2. The positive effect of population density on ASF case probability was stronger at locations near previous ASF incidents. ASF was more likely to occur in forested areas, with the probability of detecting an ASF positive sample rising from 2 to 11% as forest cover around the sample increased from 0.5 to 100%. This pattern was consistent at both low and high wild boar densities. Indicators of human activity were poor predictors of ASF occurrence. Disease control efforts, such as culling and carcass search, should be focused on high-density populations where chances of detecting and eliminating ASF-positive wild boar are higher. The intensity of control measures should decrease with distance from the infected area to match the observed spatial pattern of ASF case probability. Woodlands represent areas of the highest risk of ASF case occurrence. Distribution and connectivity of suitable habitats over the landscape can be used to prioritize disease-management actions.

1. Introduction

Landscape structure influences the movement and distribution of animal hosts, determining pathogen transmission rates and, consequently, shaping spatial variation in occurrence and dynamics of infectious diseases. The size and connectivity of suitable habitat patches may either constrain (Smith et al., 2002) or facilitate (Langlois 2001; Page et al., 2001) disease spread and persistence. Habitat quality can also affect the densities of host populations, which is another key parameter in the dynamics of many wildlife diseases (Lloyd-Smith et al., 2005; Rossi et al., 2005). Therefore, landscape structure and host abundance often have an interactive effect on disease occurrence (Kramer-Schadt et al., 2009; Habib et al., 2011). Ultimately, however, the distance between infected and susceptible individual is one of the most important predictors of disease transmission probability (e.g.

Rossi et al., 2005). Landscape and host population variables determining the speed at which this distance is covered are key components in spatial disease dynamics. Identifying these variables increases our ability to understand patterns of disease spread, predict epidemiological risks, and plan preventive measures (Ostfeld et al., 2005).

African swine fever (ASF) is a contagious viral disease which affects wild and domestic suids. With lethality approaching 100% and with no effective treatment or vaccination, the disease represents a major threat to pig production and wildlife host populations worldwide (Costard et al., 2009; Costard et al., 2013). Until the middle of the last century, ASF occurred in sub-Saharan Africa, and then spread to Europe, the Caribbean, and South America, and then eradicated from all of these areas (except Sardinia) by the mid-1990s (Costard et al., 2009). This turn of events caused severe socio-economic losses related to control and eradication programmes. In 2007, ASF was accidentally introduced

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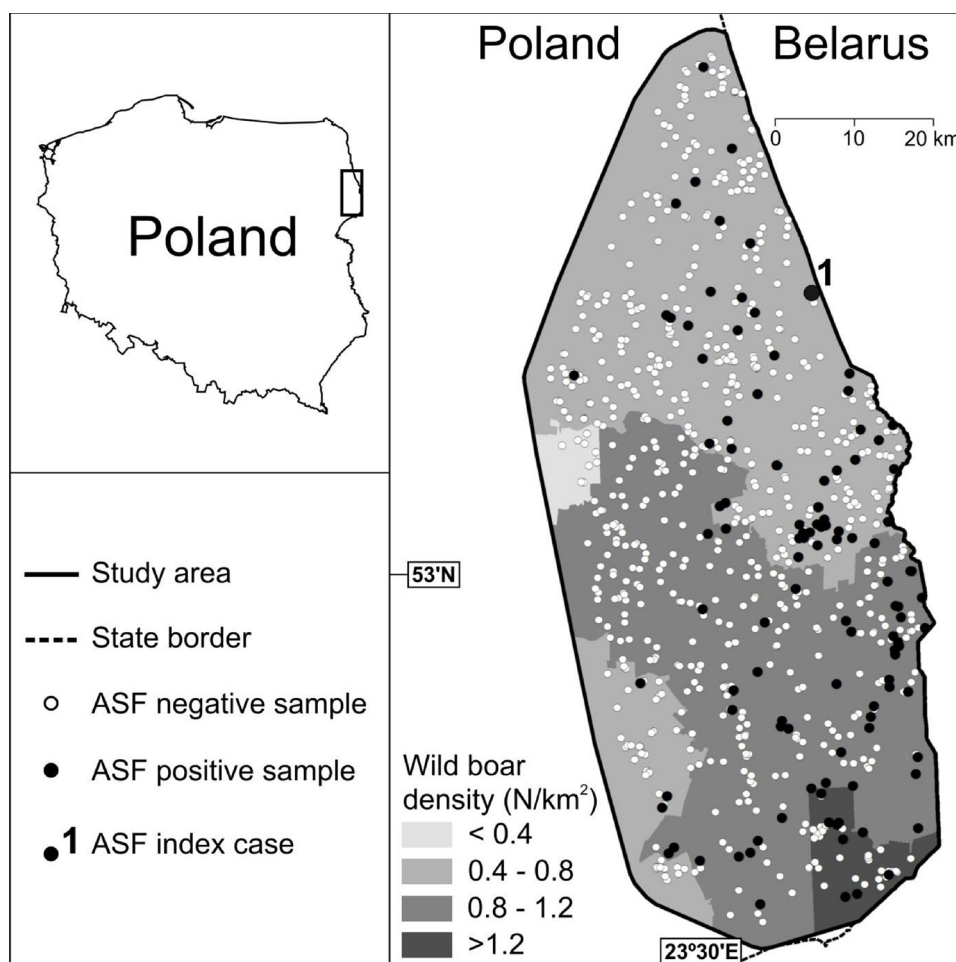 *E-mail address:* t_podgorski@ibs.bialowieza.pl (T. Podgórski).

Fig. 1. Distribution of wild boar samples used in this study located in the African swine fever (ASF) affected area in Poland, 2014-2016.

to Georgia and subsequently expanded across Armenia, Azerbaijan, Belarus, the Russian Federation, and Ukraine, and eventually entered the European Union in 2014, where it has been spreading throughout Estonia, Latvia, Lithuania, Poland, and more recently Belgium, Bulgaria, Czech Republic, Hungary and Romania (Śmietanka et al., 2016; Woźniakowski et al., 2016; Chenais et al. 2019). Recent studies (Oļševskis et al., 2016.

; Śmietanka et al., 2016; Frant et al., 2017) have indicated that wild boar (*Sus scrofa*) is the sole wildlife reservoir of ASF virus (ASFV) in Eastern Europe, able to maintain the disease independently from domestic pigs or other sources of infection (Chenais et al., 2018), a situation neither observed before nor anticipated in the future (Laddomada et al., 1994; Mur et al., 2012). Due to the novelty of ecological setting, factors underlying spread of ASF in free-ranging wild boar have not been systematically studied and remain largely speculative.

There are three major groups of putative factors influencing the incidence of ASF in wild and domestic pig populations. The first group includes abundance and distribution of the host, which determine the number of susceptible animals and their spatial variation. Wild boar is an abundant game species across Europe, but its densities exhibit a high spatial variation (Andrzejewski and Jezierski, 1978; Apollonio et al., 2010; Borowik et al., 2013). The second group of factors includes landscape variables shaping spatial variation in wild boar numbers and, indirectly, the ASF incidence. Habitat composition plays a crucial role in wild boar count variation, with forested areas representing the most suitable habitats as reflected by the highest densities (Borowik et al., 2013; Bosch et al., 2017). Thus, the proportion of suitable habitat can be used to predict epidemiological risk (Bosch et al., 2017; EFSA

(European Food Safety Authority) et al., 2017). Next to sustaining high population numbers, suitable habitats can create conditions for indirect transmission of ASFV, such as through infected carrion or environmental contamination, which play important roles in ASF epidemiology (Costard et al., 2013). Finally, the third group of factors relates to how human activities influence the spread of ASF. ASFV can be transmitted via variable fomites, such as contaminated clothing and equipment, as well as infected meat products. This particularly underlines the risk of human-mediated spread as a result of poor biosecurity of pig husbandry and wild boar hunting (Wieland et al., 2011; Costard et al., 2013). Indeed, humans as a vector continues to play a critical role in ASF spread in affected countries, particularly over long distances, despite implemented preventive measures (EFSA et al., 2017).

In this study, we evaluated the role of these three groups of factors in shaping the probability of ASF case occurrence in free-ranging wild boar using three years of epidemiological data from Poland. The ASF epidemic in the wild boar population in Poland initiated in February 2014 with the first case detected in the north-eastern part of the country, < 1 km from the border with Belarus, and has subsequently spread westwards from and along the border. In 2014-2015 during the first 18 months of the epidemic, ASF prevalence was 18.6% in wild boar found dead and 0.2% in hunted animals (Śmietanka et al., 2016). We expected that the probability of ASF cases occurrence would be positively related to 1) wild boar density because higher number of hosts increase transmission, 2) proportion of forest cover due to higher rates of direct and indirect transmission in suitable habitat, 3) indicators of human activity (road density and built-up area) because people can facilitate ASF transmission through non-compliance to hunting and

farming biosecurity measures, 4) proximity to the source of infection (distance to previous ASF cases and to the border with Belarus, where the index case was located). Furthermore, we predicted that the positive effects of habitat composition and proximity to previous ASF cases on ASF case probability would be stronger at higher wild boar densities. We suspected that at high densities, greater numbers of susceptible individuals would enhance transmission closer to the source of infection and in suitable habitats, where wild boar movements and contacts are not restricted by landscape structure. At low densities, the effects of the distance-to-infection and habitat variables would be offset by small numbers of susceptible individuals.

2. Material and methods

2.1. Study area and epidemiological data

The study area (3615 km^2) was defined as 100% minimum convex polygon enclosing locations of all samples used in the analyses with 3 km wide buffer (Fig. 1). The area is largely a field-woodland mosaic characterized by extensive agriculture, low human population density (60 people/km^2), and a relatively high proportion of forest cover (31%). The landscape is flat (highest elevation 298 ms a.s.l.) with no significant natural or man-made barriers to wild boar movement. The wild boar population is continuous throughout the area, with densities at the start of the epidemic varying from 0.5 to 5 in.s/km^2 at a forest district level (Regional Directorate of State Forests, Białystok, Poland).

We used surveillance data routinely collected by the National Reference Laboratory for ASF at the National Veterinary Research Institute in Puławy, Poland. Briefly, the total DNA was extracted from all collected samples using QIAamp DNA Mini Kit (Qiagen, Hilden, Germany). Next, real-time PCR with an UPL probe (Sigma-Aldrich, Germany) was applied to detect DNA virus presence. The sensitivity of this assay was 5 copies of ASFV DNA. Parallely, wild boar sera were tested using ELISA Ingezim PPA Compac, K3 for antibody presence and confirmed using immunoperoxidase test (IPT) (EURL, Valdeolmos, Spain). Detailed descriptions of surveillance design and laboratory procedures can be found in Fernández-Pinero et al. (2012), Woźniakowski et al. (2016) and Śmietanka et al. (2016). We defined case as an individual wild boar testing positive for ASF virus in real-time PCR. Hereafter, we use "sample" as equivalent of individual animal. Here we used data on 895 wild boar samples (181 positive, i.e. cases, and 714 negative) collected in 2014-2016 in a study area for which precise spatial locations were available (Fig. 1). We selected just one data point from locations with multiple animals available, e.g. several individuals found dead together. This procedure reduced the number of analysed cases from 181 to 116 and did not change the number of non-cases (n = 714). The analysis included 84% of all ASF cases detected in Polish wild boar during the study period. The remaining 16% of cases were located in two isolated clusters about 100 km away from our study area. These clusters resulted from a spillover from domestic pigs in late 2016.

2.2. Geographic and population parameters

We created a 2 km radius buffer around the location of each sample to reflect the home range size occupied by the sampled animal in the study area (Podgórski et al. 2013, Podgórski et al. 2014). Then, for each sample we recorded the following variables: 1) proportion of forest cover within the buffer area, 2) proportion of built-up area within the buffer, 3) aggregated road length within the buffer (national, regional, and local roads pooled), 4) shortest distance from the sample location to the border with Belarus, 5) mean distance from the sample location to all previous wild boar ASF cases. Sampling date was used to order cases in time. Forest cover, built-up area, and road lengths were calculated based on the Database of Topographic Objects BDOT10k (Head Office of Land Surveying and Cartography, Warsaw, Poland) using

vector maps with the data from 2012-2013 and spatial resolution of 30 m^2. Estimates of wild boar density, based on annual driven counts routinely performed in late winter (pre-reproductive) by the State Forests - National Forest Holding, were available for 10 forest districts covering the study area (Regional Directorate of State Forests, Białystok, Poland). Based on its spatial location, each sample was assigned the density value of the corresponding forest district, averaged over the study period (Fig. 1). Spatial analyses were conducted using Arc View GIS 9.1 (ESRI, Redlands, California).

2.3. Statistical analysis

Effect of time elapsed from the first occurrence of ASF in Poland on the probability of ASF case was investigated with generalized additive models (Hastie and Tibshirani 1990, Hastie 1992) using package 'gam' of the R program. Linear effect of time was fitted to surveillance data to analyse general temporal trend in the ASF case probability, while non-linear effect of time was used to explore seasonal variation. Here we used all surveillance data available for the study period and area (181 ASF-positive samples and 8725 ASF-negative), aggregated at the smallest administrative units.

We analysed the effects of explanatory variables on the probability of ASF case using generalized mixed-effects models with a binomial response (status of each sample; 0: ASF-negative, 1: ASF-positive) and "logit" link function (Zuur et al., 2009, Bates et al., 2015). Probability of ASF case refer to a chance of any sampled individual from the study area testing positive to ASF. None of the explanatory variables were substantially inter-correlated (R < 0.41). Hence, the global model included main effects of all considered variables: forest cover, percentage of built-up area, road length, distance to the border, mean distance to previous ASF cases, wild boar density, as well as interactive effect of wild boar density with forest cover and wild boar density with mean distance to previous ASF cases. Prior to modelling, all explanatory factors were standardized by subtracting the mean from the variable value and then dividing by standard deviation (Grueber et al., 2011). Here we used only samples with precise spatial locations (XY coordinates): 116 cases and 714 non-cases.

We detected significant spatial autocorrelation in the data by applying a variogram to residuals of the full model with fixed effects only (range: 3952 metersms, nugget: 0.603). To minimize the effects of spatial autocorrelation we created a 2 × 2 km spatial grid covering the study area and used grid cell ID as a random factor in subsequent modelling procedures (Zuur et al., 2009). Following these steps, spatial autocorrelation in the model residuals was significantly reduced (range: 12 meters, nugget: 0.008). The model accounting for spatial autocorrelation in the data (i.e. with random effect of spatial grid) provided better fit as indicated by lower Akaike information criterion (AIC) score compared to the model without the random effect (586.5 vs 600.2, respectively).

We applied model ranking on sub-models containing all possible combinations of explanatory variables with the Akaike information criterion (AIC) with a second-order correction for small sample size (AIC$_c$). The differences between AIC$_c$ scores among highly ranked models were low (ΔAIC$_c$ < 1), therefore we did not select a single best model. Instead, we averaged models from the selected confidence set of sub-models (cumulative model weights (ωi) ≤ 0.95; Table 1) and drew inferences based on averaged coefficients (Burnham and Anderson 2002; Bartoń, 2015). All statistical analyses were performed in R 3.3.2 (R Development Core Team, 2016).

3. Results

We found that probability of ASF case in the surveillance data did not change with time elapsed from the first occurrence of the disease in Poland (coefficient ± SE: -0.0002 ± 0.0003, P = 0.486). However, there was a significant seasonality in the probability of detecting ASF-

Table 1

Confidence set of the binomial generalized linear mixed models (GLMMs) assessing the effects of different factors* on the probability of detecting ASF case in the wild boar population in Poland, 2014-2016. Only models whose cumulative weights (ωi) were below 0.95 and an intercept model are presented.

Model	K	AIC_c	ΔAIC_c	ωi
For + Dist_bord + Den + Dist_ASF + Den × For + Den × Dist_ASF	8	583.8	0	0.161
For + Dist_bord + Den + Dist_ASF + Den × Dist_ASF	7	584.1	0.30	0.138
For + Build + Dist_bord + Den + Dist_ASF + Den × Dist_ASF	8	584.3	0.51	0.124
For + Build + Dist_bord + Den + Dist_ASF + Den × For + Den × Dist_ASF	9	584.8	0.97	0.099
For + Dist_bord + Den + Dist_ASF + Road + Den × Dist_ASF	8	585.3	1.53	0.074
For + Dist_bord + Den + Dist_ASF + Road + Den × For + Den × Dist_ASF	9	585.6	1.83	0.064
Build + Dist_bord + Den + Dist_ASF + Den × Dist_ASF	9	586.2	2.40	0.048
For + Build + Dist_bord + Den + Dist_ASF + Road + Den × Dist_ASF	9	586.3	2.45	0.047
Build + Dist_bord + Den + Dist_ASF	6	586.7	2.90	0.038
For + Build + Dist_bord + Den + Dist_ASF + Road + Den × For + Den × Dist_ASF	10	586.8	2.96	0.037
For + Build + Dist_bord + Den + Dist_ASF	7	586.9	3.08	0.034
For + Dist_bord + Den + Dist_ASF	6	587.8	3.95	0.022
Build + Dist_bord + Den + Dist_ASF + Road + Den × Dist_ASF	8	588.2	4.43	0.017
Build + Dist_bord + Den + Dist_ASF + Road	7	588.7	4.90	0.014
For + Build + Dist_bord + Den + Dist_ASF + Den × For	8	588.7	4.94	0.014
For + Build + Dist_bord + Den + Dist_ASF + Road	8	588.9	5.12	0.013
Intercept	2	610.7	26.9	0

*For – forest cover; Build – Built-up area; Road – road density; Dist_bord – Distance to PL-BY border; Dist_ASF – distance to previous ASF cases; Den – population density; K – number of estimated parameters; AIC_c – Akaike's information criterion with a second order correction for small sample sizes; ΔAIC_c – difference in AIC_c between a given model and the most parsimonious model; ωi – weight of the model. Parameter estimates of the averaged model are presented in Fig. 3.
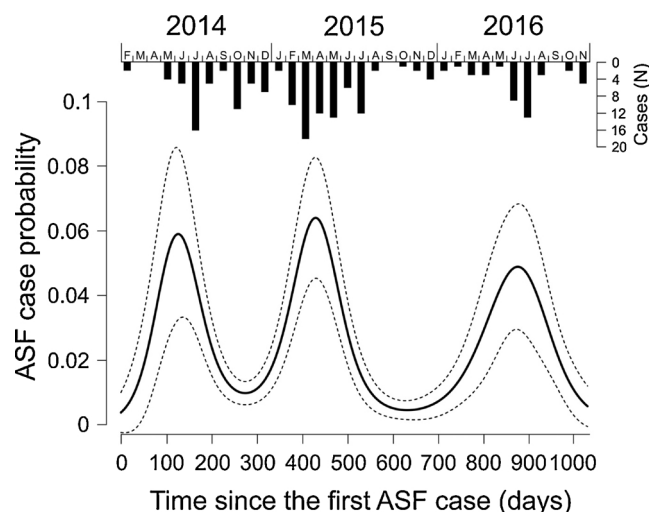

Fig. 2. Temporal trends in the number and probability of African swine fever (ASF) cases in the study area in 2014-2016. Probability of ASF case refer to a chance of any sampled individual from the study area testing positive to ASF. Solid line represents non-linear effect of time fitted to the surveillance data with generalized additive model, dashed lines represent 95% confidence intervals around the parameter estimate.
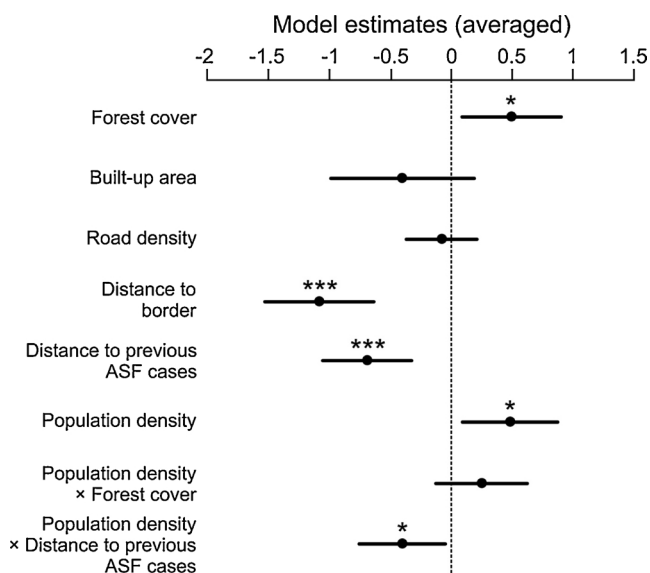

Fig. 3. Coefficients of the model explaining variation in the probability of African swine fever (ASF) case in the wild boar population in Poland, 2014-2016. Parameter estimates were obtained with generalized mixed-effects model averaged over the selected confidence set of submodels (cumulative model weights ωi = 0.95, for details see Table 1).

positive sample (coefficient ± SE: -4.188 ± 0.098, $P <$ 0.001) with distinct peaks in spring and early summer months (Fig. 2). The averaged model indicated significant positive effects of forest cover (coefficient ± SE: 0.49 ± 0.21, $P =$ 0.02) and wild boar population density (coefficient ± SE: 0.48 ± 0.20, $P =$ 0.01), as well as negative effects of distance to the border (coefficient ± SE: -1.08 ± 0.23, $P < 0.001$), mean distance to previous ASF cases (coefficient ± SE: -0.68 ± 0.19, $P < 0.001$), and interaction between population density and mean distance to previous cases (coefficient ± SE: -0.40 ± 0.18, $P =$ 0.02) on the probability of the ASF case (Fig. 3).

The buffer area (2 km radius) around ASF cases had a 59% forest cover on average. As forest cover increased from 0.5 to 100%, the probability of detecting ASF case in the study area rose from 2 to 11% (Fig. 4).The population density of wild boars over the whole study area was 0.8 in./km^2 on average. As population density locally increased from 0.4 to 2 in./km^2, the probability of detecting ASF-positive wild boar increased from 3 to 20% (Fig. 4), e.g. in an area of 100 km^2 with

density of 0.4 in./km^2, one could expect to detect 1 ASF-positive animal, while 40 ASF cases were expected in the same area with density of 2 in./km^2.

Proximity to the source of infection was an important positive predictor of ASF case occurrence. During the study period, ASF cases were located on average 10 km westward of the eastern border and expanded ca.100 km latitudinally along the border (Fig. 1). The probability of detecting ASF cases decreased by 21% with distance from the border increasing from 0.07 to 37 km (Fig. 4). The probability of detecting ASF case declined by 19% with increasing distance to all previous ASF cases increasing from 7 to 64 km (Fig. 4). This latter effect, however, was modified by the local density of wild boar. At low densities (< 1 ind./km^2), the probability of ASF case occurrence remained low regardless of the distance to previous cases. At higher densities (> 1.5 ind./km^2), the probability sharply decreased from very high in close proximity to previous ASF cases, to very low far away (Fig. 5).
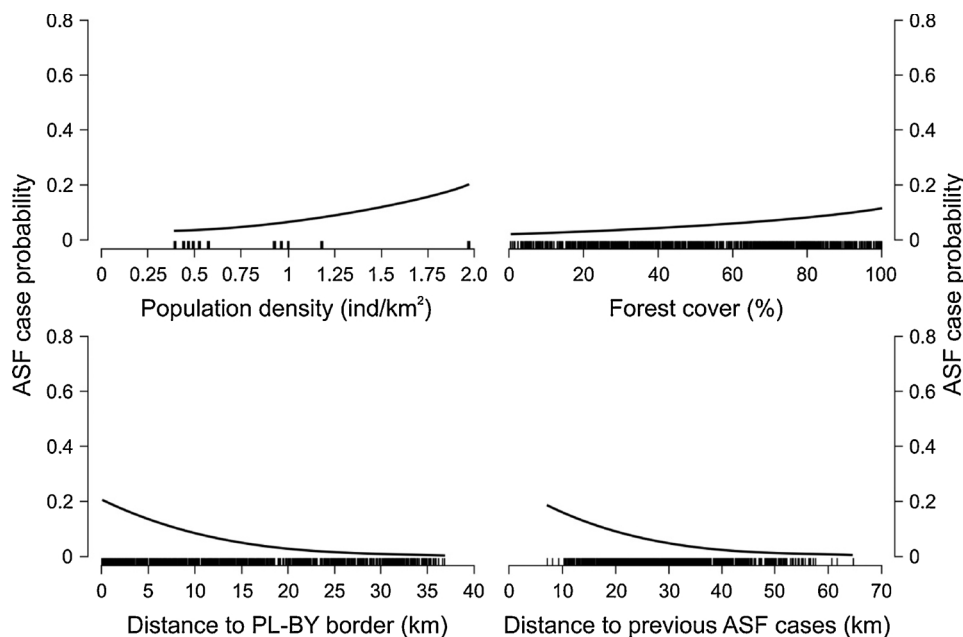
Fig. 4. Effects of population density, forest cover, distance to Poland-Belarus border, and previous ASF cases on the probability of African swine fever (ASF) case in the wild boar population in Poland, 2014-2016. Solid lines correspond to the effect estimates obtained with an averaged generalized mixed-effects model. Asterisks refer to statistical significance of the effect: *0.05 > p > 0.01; **0.01 > p > 0.001; ***p < 0.001.

We found no evidence that human-related factors shaped the variation of ASF case occurrence. Both percentage of build-up area (mean: 0.26, range: 0-2.7%) and road length (mean: 43, range: 4-85 km) around each sample had insignificant effects on ASF case probability (Fig. 3).

4. Discussion

4.1. Host density

We found a positive effect of wild boar abundance on the probability of detecting ASF case. A positive relationship between host density and disease occurrence is common in many host-pathogen systems (e.g. Rossi et al., 2005; Joly et al., 2006, Kramer-Schadt et al., 2009). Wild boar numbers and ASF occurrence were positively correlated in Estonia across a similar range of densities as in our study (Nurmoja et al. 2017). These results indicate that ASF transmission is density-dependent. Two non-mutually exclusive processes could be underlying a density-dependent pattern of ASF incidence. First, contact rates between individuals tend to increase at higher densities (Habib et al., 2011; Tardy et al., 2018), which can enhance direct disease transmission. Second, there are higher chances of indirect transmission through infected carcasses and contaminated environment when the number of animals (susceptible, infected and dead) is large. We found a continuous decline in the ASF case probability along the five-fold gradient of host densities, reaching 3% at the lowest density (0.4 ind./km^2). Wild boar density may not be an ultimate factor limiting ASF persistence due to long availability of the virus in infectious carcasses, which then offsets the density-dependent transmission at low host densities and enables the virus to persist in the environment (Chenais et al., 2018). In fact, epidemiological data from affected EU countries show long-term persistence of ASF (EFSA et al., 2017; Śmietanka et al., 2016).

The positive effect of population density on the probability of detecting ASF case was stronger at distances closer to previous ASF cases. At low densities, the chance of ASF case was low, regardless of the distance to affected sites. At high densities, case probability was very high in close proximity to previous cases, but declined sharply as this distance increased and equalled the probability for low density populations 40 km away from the affected area. Past this distance mark, population density had no effect on ASF incidence which suggests

optimal spatial scale for implementation of disease control measures. Our density estimates were available at relatively coarse spatial scale of forest district and it is possible that local variation in densities between habitat patches could slightly modify this relationship at even finer spatial scale. Nevertheless, these results, showing quick decay of ASF case probability with distance from previous infections, indicate that the spread of ASF in wild boar populations is slow and spatially limited even at high densities. This pattern can be attributed to the constraints on ASF transmission imposed by wild boar social systems and disease characteristics (Podgórski et al., 2018; Podgórski and Śmietanka, 2018). Interestingly, a strong positive effect of population density on disease incidence near the infected area was also observed for classical swine fever in wild boar (Rossi et al., 2005) and chronic wasting disease in white-tailed deer *Odoceoileus virginianus* (Joly et al., 2006). Both diseases share hosts of similar social organization (stable matrilineal social units), which could help explain the apparent parallels in spatial epidemiology of these different host-pathogen systems.

4.2. Landscape structure

Our results showed that ASF is more likely to occur in forested areas and thus highlighted the role of habitat composition in the epidemiology of the disease. In central and eastern Europe, forests represent optimal wild boar habitats and sustain high population numbers (Borowik et al., 2013; Bosch et al., 2017). At the regional scale of our study, however, wild boar density and the proportion of forest cover were not correlated, and we believe that our forest cover variable is best interpreted as an index of habitat fragmentation. Landscape heterogeneity can have significant effects on the dynamics of wildlife diseases. For example, classical swine fever in wild boar shows higher incidence and persistence in large and well-connected forests than in small and isolated patches (Rossi et al., 2005; Kramer-Schadt et al., 2009). Low habitat fragmentation allow unrestricted movement of animals and high contact rates between susceptible and infectious individuals, thus enhancing disease persistence and spread. In our study, wild boar inhabiting areas with continuous forest cover were more likely to be ASF positive than those living in the fragmented landscape of a field-forest mosaic. Our results are consistent with previous findings showing correlation of ASF incidence and habitat quality (Bosch et al., 2017; EFSA et al., 2017).

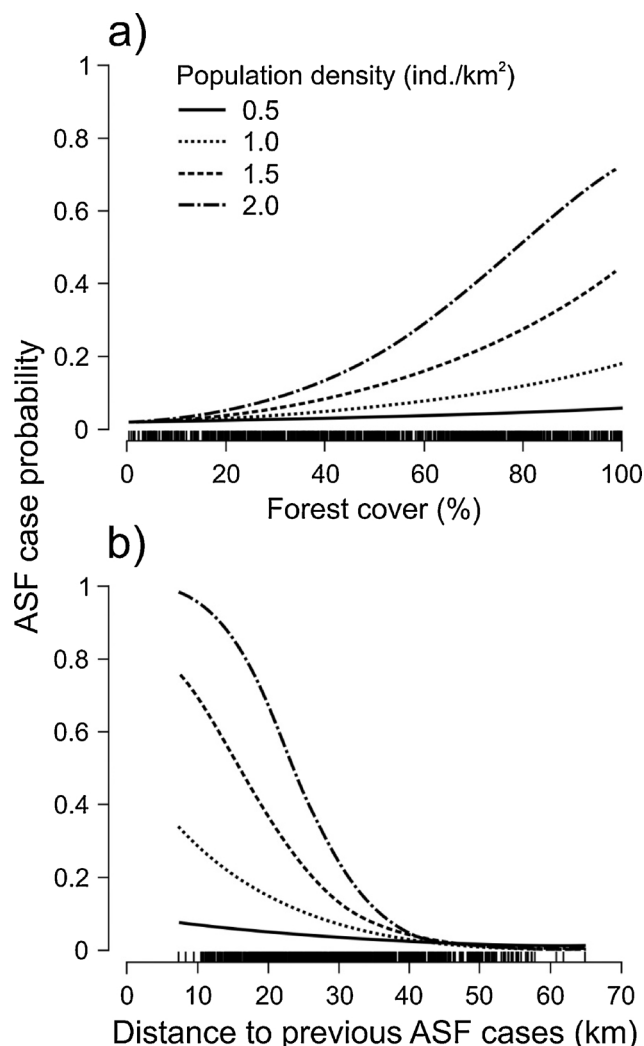These results indicate that disease surveillance and control

Fig. 5. Interactive effects of (a) proportion of forest cover around the sample and wild boar population density, and (b) distance to previous African swine fever (ASF) cases and wild boar population density on the probability of ASF case in the wild boar population in Poland, 2014-2016. Only the interactive effect in (b) was statistically significant (p = 0.02).

programmes should target large patches of suitable habitats to effectively reduce the number of infected individuals (dead or alive) and limit disease spread. Habitat composition can be seasonally variable and that a suitable wild boar habitat during one season, e.g. maize fields, can turn into a less suitable one during others, e.g. non-cultivated open fields (Keuling et al., 2009; Thurfjell et al., 2009). This seasonal dynamics should be considered in areas where wild boar utilize different habitats according to seasonal availability of resources. Interestingly, the positive effect of forest cover on the probability of detecting ASF cases was consistent both at low and high wild boar densities, underlying the importance of landscape structure in understanding disease dynamics and planning control actions.

4.3. Human activity

We found that indicators of human activity (proportion of built-up area and road density) were, contrary to our expectations, poor predictors of ASF case probability. During the study period, only four ASF outbreaks in domestic pigs occurred in the study area. There was no evidence of spillover from domestic pigs to wild boar according to the epidemiological investigations carried out by competent veterinary authorities. Human-mediated transmission via fomites (clothing,

equipment) and poor biosecurity during hunting can enhance local spread of the ASF virus within wild boar-habitat epidemiological cycles without intersecting with domestic cycles (Śmietanka et al., 2016; Chenais et al., 2018). Nevertheless, it seems that the impact of human-mediated transmission on spatial dynamics of the disease was limited in our study.

Anthropogenic spread continues to play a critical role in ASF expansion in affected countries of the European Union despite all preventive measures implemented. Human-mediated transmission enables fast and long range spread, resulting in a large-scale discontinuous distribution of isolated case clusters (EFSA et al., 2017; Stokstad, 2017). Analysis of epidemiological data from Estonia revealed a positive effect of human activity (approximated by road network density and number of pig farms) on the probability of ASF occurrence in wild boar (EFSA et al., 2017). Impacts of human activity on ASF dynamics can vary locally depending on human compliance to biosecurity, wild boar management, and pig farming systems. This diversity should be considered in ASF risk assessments and control efforts.

4.4. Temporal trends

We found that probability of ASF case did not change with time elapsed from the first occurrence of the disease indicating that prevalence was stable over time. Similar pattern was found in Latvia (Schulz et al. 2019) and northern Estonia (Nurmoja et al. 2017). This course of ASF epidemic can be partly attributed to its low contagiousity and long-term persistence in natural conditions, leading to an endemic state where environmental contamination enables extended transmission cycles in not fully depleted host population (Chenais et al. 2019). Our data showed high seasonality in ASF case probability with distinct peaks in spring and summer. Seasonal pattern with similar spring-summer peaks in ASF prevalence was reported in north-eastern Poland previously (Śmietanka et al. 2016). Increased incidence rate in spring and summer can possibly result from higher number of susceptible hosts following spring reproduction and higher visitation rates at carcass in summer (Probst et al. 2017).

5. Conclusions

Our work attempted to identify factors underlying spread of ASF in free-ranging wild boar, which are crucial for mapping and managing epidemiological risks. First, wild boar density had a positive effect on the probability of disease occurrence. Thus, disease control efforts should be focused on high-density populations where the chances of detecting and eliminating ASF-positive wild boar, either through culling or carcass searches, are higher. However, as there is no evidence of a population threshold for spontaneous ASF fade-out, ideal target density level remains in question. Second, our results indicate that disease control efforts should be concentrated close (< 40 km) to infected areas where risk of ASF occurrence is the highest. The intensity of control measures should decrease with distance from the infected area to match the observed spatial pattern of ASF case probability. Third, risk of ASF case occurrence varies over the landscape depending on habitat composition. Large woodlands represent areas of the highest risk, which decreases the smaller and more fragmented a habitat becomes. Distribution and connectivity of suitable habitats over the landscape can thus be used to structure and prioritize disease-management actions. Lastly, our inferences may be biased by the local conditions of north-eastern Poland and may not necessarily apply to other countries where ASF spreads in the wild boar populations.

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