Could wild boar be the Trans-Siberian transmitter of African swine fever?

Fekede Joka[1], HaoNing Wang[2], Hein van Gils[1], and Wang Xiaolong[1]

[1]Northeast Forestry University
[2]Harbin University

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Abstract

African swine fever (ASF) free China has experienced a sudden multi-focal and multi-round of outbreaks during 2018. The subsequent epidemiological survey resulted in a debate including the possibility of a transboundary spread from European Russia to China through wild boar. We contribute to the debate by assessing a potential Trans-Siberian transmission path and its associated ASF arrival dates. Least Cost Paths (LCPs) between Eastern Europe and NE China were plotted. The arrival dates of ASF-infected wild boar have been predicted by cumulative maximum transmission distances per season and cover with their associated minimum time intervals along the LCPs. Our results show high costs for wild boar to cross Xinjiang, NW China and/or Mongolia to reach NE China. Instead, the Paths lead almost straight eastward along the 59.5° Northern latitude through Siberia and would have taken a minimum of 219 or 260 days.

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INTRODUCTION

African swine fever (ASF) is a notifiable, highly contagious and fatal viral disease both wild and domestic suids. The ASF virus (ASFV) was endemic in Sub-Saharan Africa for nearly 40 years (1921-1957) before it was transmitted to Europe (Montgomery 1921; Mulumba-Mfumu *et al.*2019). In the 1960s, the ASFV was identified in Portugal and Spain (Mur*et al.* 2012). Thereafter, sporadic ASF outbreaks occurred until 1995 in a few west European countries (Cwynar *et al.* 2019). Only on the Italian island Sardinia, the disease remained endemic till today (EFSA 2010). Since 2007, ASFV strains spread from Transcaucasia (Georgia) across the Caucasus Mountains into the Russian Federation (RF) and neighbouring Eastern Europe (Costard *et al.* 2013). These strains are highly virulent and induce an acute form of the disease (Gabriel *et al.* 2011). However, a few infected wild boar individuals may remain asymptomatic or recover, thus becoming a carrier and contributing to dispersal of the virus (Gallardo *et al.* 2015; Pautienius *et al.* 2018).

ASF may be transmitted by direct and/or indirect physical pig-to-pig contact and human activities. For anthropogenic transmission, the following pathways have been suggested: unregulated long-distance transport by road and maritime shipping lane of infected pork products and pigs, swill originating from aircraft and ships, smuggled pork, home slaughter and wild boar hunting as well as farming practices. In sub-Saharan Africa, a sylvatic transmission cycle of ASF is sustained by warthog (*Phacochoerus aethiopicus*) and bushpig (*Potamochoerus spp* .) (Kleiboeker *et al.* 1998; Bastos*et al.* 2004). In the northern hemisphere, the wild boar-habitat cycle is the main concern (Guberti *et al.* 2018) for ASFV transmission, because mobility of wild boar between regions and countries is largely uncontrolled (Śmietanka *et al.* 2016). Eurasian wild boar is associated with three land cover types, namely broadleaved deciduous forest, mixed forest and cropland as well as elevation and slope angle (Fonseca 2008; Keuling *et al.* 2009; Xu*et al.* 2011; Zhu *et al.* 2011) .

The ASFV-free situation in Asia ended suddenly on 02 August 2018, when ASF was diagnosed for the first time in China; in the NE (Zhou *et al.* 2018). It marked the start of an epidemic affecting the pig industry over large stretches of China Cambodia, Hong Kong, Mongolia, North Korea and Vietnam (Le *et al.* 2019; OIE 2019) within 9 months. Since the first ASF case in NE China, the source of the infection has been debated (Zhou *et al.* 2018; Bao *et al.*2019), but remains unclear (Shao *et al.* 2018). The DNA sequence homologies between isolates from China and Europe (Bao *et al.*2019) suggest a source in Eastern Europe. Natural or anthropogenic long-distance transmissions have been suggested. Alternatively, assumed wholesale contamination of the RF with ASFV is put forward as the source. At the other end of the debate, it is argued that the Irkutsk case (FAO 2018) at about 3000 km from Eastern Europe and 1000 km from NE China, or a similar, but undiagnosed infection could have been the source. However, in such scenario we would have seen a progressive expansion of outbreaks in domestic pig across Siberia, followed, most probably, by a wave of infections in wild boar across NE China given their unhindered cross-border movements.

ASFV isolated from wild boar in Heilongjiang (HLJ) and Jilin (Li*et al.* 2018), as well as domestic pig in the Liaoning (Ge*et al.* 2018; Zhou *et al.* 2018) and Anhui provinces (Bao*et al.* 2019) in China belong to the European genotype II and serotype 8. ASF in China has been mainly diagnosed in domestic pig, but also in wild boar in the Changbai Mountains on 16 November 2018 (Li*et al.* 2018) and in Heihe on 28 November 2018 (OIE 2018). Further, our sampling at 78 wild boar farms in NE China over the past 4 years never yielded positive results for ASFV (Li et al., 2018). In the absence of direct evidence, the debate continues among vets, research institutes, the pig industry and residents (www.virology.com.cn). The outbreak on the 30 July 2019 in Shirokaya in the Far East of the Russian Federation added new information and an additional perspective to the debate, namely that the infection might be caused by cross-border movement of infected wild boar from China (http://sputniknews.cn/society/201908141029275692/). As a contribution to the discourse, we test the following alternate hypotheses. ASF may have been transmitted by ASF-infected wild boar from Eastern Europe through Central Asia and/or across Siberia to NE China versus ASF has been transmitted through other trajectories.

Our research area consists of the Source (Eastern Europe), the Transmission (Siberia, Central Asia, NW China and Mongolia) and the Impact region (NE China). We extrapolated the occurrence points of ASF-infected wild boar in the Source region across the three regions with a maximum entropy algorithm (MaxEnt) to identify highly suitable areas in the Impact region. Next, we developed a cost surface for wild boar dispersal through the Transmission region using the Spatial Distribution Modeller (SDM) of ArcGIS 10.3. The distribution model and the cost surface were both based on land cover type - cover from hereon - elevation and slope angle. Through the cost surface, Least Cost Paths (LCPs) were established again using the SDM. LCP-slope and LCP-elevation were developed through alternate input of slope angle and elevation separately as the Transmission region contains higher mountains and larger plains than the Source region. Subsequently, we segmented the LCPs in stretches homogeneous for cover and season to attribute to each stretch the cover- and season-specific maximum transmission distances and minimum transmission time intervals as calculated for the Source region. Finally, we summated the obtained time intervals of all LCP segments to estimate the earliest possible arrival time of the ASFV in the Impact region. Finally, we compared the predicted with the actual arrival date.

MATERIALS AND METHODS

Research area and input data

The research area covers broadly the northern Eurasian continent between the Arctic Circle and the 35° Northern latitude. Within northern Eurasia, we distinguished three regions: the ASF Source region (Eastern Europe), the hypothetical ASF Overland Transmission region (Siberian portion of the Russian Federation, Central Asia, NW China, and Mongolia) and the ASF Impact region (NE China). Eastern Europe includes the following countries with ASF-infected wild boar: Estonia, Latvia, Lithuania, European Russia, Czechia, Hungary, The Ukraine, Poland and Romania. We extracted all dated point locations within the Source region between 05 December 2007 and 25 December 2018 of ASF-infected wild boar (n=7383) from the OIE website (www.oie.int). For the three regions, the elevation layer at 30 arc-second resolution was downloaded

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from the global land cover facility (www.landcover.org) and cover at 300 m spatial resolution from the European Space Agency (ESA: www.maps.elie.ucl.ac.be/CCI/viewer). We derived the slope angle (%) from the elevation raster. Administrative boundaries were downloaded as shapefiles from DIVAGIS (www.diva-gis.org).

Our prediction depends on the following assumptions:

1. The ASF transmission as addressed relies exclusively on movement of ASF-infected wild boar
2. The wild boar density along the Least Cost Path is high enough for transmission

Research approach

Cover, elevation and slope were attributed to the unfiltered ASF-infected wild boar occurrence locations in Eastern Europe. We capped the distance that an individual wild boar may seasonally disperse per cover type at 150 km based on the literature (Singer *et al.* 1981; Keuling *et al.* 2010; Jerina *et al.* 2014). For transmission distance and time interval estimation, we sequenced the records of ASF-infected wild boar occurrence from European Russia (n=383) by observation date and season (Thurfjell *et al.* 2014). The latter were defined as follows: winter (December, January, February), spring (March, April, May), summer (June, July, August), autumn (September, October, November) (www.seasonsyear. com/Russia). Subsequently, we merged point locations with the same date and geographic coordinates. Transmission time intervals shorter than 4 days were excluded (Beltrán-Alcrudo *et al.* 2017). Next, we connected the point location of each record by a line to its nearest spatial neighbour (Ward*et al.* 2008) occurring within 12 months. After 12 month (4 seasons), the later infection may be considered unrelated to the previous (Adkin *et al.* 2004; Cortiñas Abrahantes *et al.*2017), considering the retention period of ASFV infectivity in winter-frozen wild boar carcasses that may persist at least 6 months (Cortiñas Abrahantes *et al.* 2017)· Then, we projected the point map to Azimuthal Equidistant World and calculated the geometric transmission distance (km) in ArcGIS and the time interval (days) in Excel. For all points, the season was derived from the observation date and the cover by overlay with the ESA cover map. The frequency, maximum distance and minimum time intervals were calculated and their relationship evaluated by a scatter plot in SPSS v25.

An environmental suitability model for ASF-infected wild boar covering the Source, Transmission and Impact region, based on the presence points of ASF-infected wild boar, cover (type), elevation (m) and slope angle (%) was generated with MaxEnt version 3.4.1(Phillips *et al.*2017). To minimize spatial autocorrelation (Mark & Fortin 2002), we filtered the ASF-infected wild boar occurrence points (n= 7383) (Tables S1) using the SDM Toolbox v1.1c (Brown 2014) integrated into ArcGIS. ASF-infected wild boar records were spatially rarefied, at a minimum distance of 10 km between each pair of presence points (Fekede*et al.* 2019). Then, we entered the filtered presence points and the environmental variables into MaxEnt followed the procedure of a previous study (Fekede *et al.* 2019). The resulting suitability model was used to select high suitability endpoints of the LCP at the border of the Impact area.

Least Cost Paths through the Transmission region for ASF-infected wild boar

We created a cost/resistance surface for ASF-infected wild boar dispersal in the Transmission region using reclassified cover, elevation and slope as cost factors. We used the Spatial Data Modeller toolbox in ArcGIS that strings together sequences of geoprocessing tools, feeding the output of one tool into the next. The reclassification followed the Jenks natural breaks method (De la Torre *et al.* 2013) providing a common measurement scale of 1 (no resistance) to 10 (highest resistance) for all three cost factors (Wang *et al.* 2009; Hashmi *et al.* 2017). The three were then combined through a logical overlay operation (Wang *et al.* 2009; Hashmi *et al.* 2017). For the LCPs, the starting point was the most eastern ASF-infected wild boar occurrence in the Source region (Fig. 5; coordinates: 46.617933, 55.253717) and the endpoint the most northwestern highly suitable area in the Impact region (Fig. 4; Fig. 5). Finally, two least-cost paths, LCP-slope and LCP-elevation, were generated (Wang *et al.* 2009) through alternate input of slope and elevation separately (Fig.5).

Potential ASF-infected wild boar arrival time in NE China

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We projected the line map of both LCPs to Azimuthal Equidistant World and calculated their geometric distances (km). Progressing eastward from the LCP starting point, we determined the cover and season along the LCPs till the point where one of the two changed. Then, the procedure was repeated till the endpoint in the Impact area. Each of the obtained homogeneous stretches for cover and season was attributed with its specific maximum distance and minimum time interval (Table 2). We summed the time intervals of the homogenous stretches to obtain the minimum time required to move along the LCP.

RESULTS

Occurrence of ASF-infected wild boar

The occurrence of ASF-infected wild boar in the Source region was found to be primarily associated with broadleaved deciduous forest, conifer forest, mixed forest, grassland and cropland (Fig. S1, Table 1) as expected from findings reported in the literature. The association with cover was further supported by its predictive power in our suitability model for ASF-infected wild boar (Fig. S2). Beyond the cover, ASF-infected wild boar occurrence was found to be associated with low elevation: 128 m $\pm$ 93.2 SD (Fig. 1) as anticipated. In addition, the response curve generated by our suitability model showed an inverse relationship between the probability of ASF-infected wild boar occurrence and elevation (Fig. 2).

Transmission distance (km) and time interval (days)

The spatial sequencing of occurrence points and subsequent removal of duplicates left 220 ASF-infected wild boar occurrences in Eastern Europe for the transmission distance and time interval estimation. The seasonal spatiotemporal analysis in the Source region showed mostly a relatively short transmission distance ($<$ 25 km) and a small number of days ($<$ 34) (Fig. S3, S4). The highest maximum transmission distance occurred during summer in all three covers. The minimum time intervals were very similar during all seasons across covers (Table 2). The association between transmission distance and time interval was negligible (R^2=0.002) (Fig. 3).

Eastward transmission of ASF by wild boar following a Least Cost Path

The filtering for the suitability model development retained 1159 occurrence points. The first highly suitable area for ASF in wild boar in NE China coming from Siberia was predicted in the HLJ Province; the second in the Jilin Province and the third in SE Liaoning (Fig. 4). The contribution of the slope angle to the suitability is insignificant ($<$2%) compared to cover (75.4%) and elevation (22.9%).

The LCP-slope and LCP-elevation are presented in Fig. 5. The LCP-slope starting in the Caucasus region leads directly up north, then eastward across West Kazakhstan and joins the LCP-elevation east of the Ural Mountains. Our LCPs show that it is costly for wild boar to cross Mongolia and the Xinjiang Uygur Autonomous region in NW China. The two LCPs starting at the most eastern occurrence of ASF-infected wild boar lead almost straight eastward along the 59.5° Northern latitude, crossing the Ural Mountains, the West Siberian Plain and the Central Siberia Plateau, but follow diverging paths north of Lake Baikal. The LCP-elevation remains at low elevations by following a northern path along the Lena River around the Stanovoy Mountains and then in a south-eastern direction around the Skalisty Mountains to NE China. The LCP-slope continues to head eastward and skirts Lake Baikal at its northern tip, as does the Trans-Siberian Railway, through small mountain valleys in a direct, shorter path to NE China (Fig. 5). The LCPs and the Trans-Siberia Railway run parallel to each other and intersect before Tyumen and twice around Irkutsk. The predicted earliest arrival dates in NE China for ASF-infected wild boar along the LCP-slope and LCP-elevation were 219 days (12 March 2019) and 260 days (22 April 2019) respectively.

DISCUSSION

Our findings on the association of ASF-infected wild boar with forest, cropland and their mosaics corroborates reports from Poland (FAO 2013; Śmietanka *et al.* 2016; Podgorski & Smietanka 2018). Although in Eastern Europe ASF-infected wild boar generally occurs year-round at low elevation (Fig. 1, 2), obviously wild boar may roam during summer at higher elevation (Cheng *et al.* 2013; FAO 2013). The limited wild

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boar movement during winter and spring in cropland, as identified corresponds generally with findings from Sweden, where wild boar moves along narrow landscape elements in agricultural areas (Thurfjell*et al.* 2009, 2014). However, wild boar moves in Sweden over larger distances during spring than in winter (Thurfjell *et al.*2014), contrary to our findings. Across seasons and covers, we found larger maximum transmission distances in Eastern Europe than the maximum dispersal distance in Spain and Slovenia (Casas-Diaz *et al.* 2013; Jerina *et al.* 2014).

Our result showed comparatively low maximum transmission distances of ASF-infected wild boar in all three covers during spring and winter (Table 2). This may be explained by food availability and snow depth respectively. The highest maximum transmission distance was found in summer as in Sweden (Thurfjell *et al.* 2014). Nevertheless, a few ASF-infected wild boars in Eastern Europe covered a long distance (>100 km) within a short time interval (Fig. 3: lower right corner), maybe due to anthropogenic disturbance including drive hunting (Scillitani *et al.* 2010; Said *et al.* 2012; Cortiñas Abrahantes *et al.* 2017; Fattebert *et al.* 2017). Elsewhere, undisturbed wild boar disperse over a mean linear distance of 45.8 km and maximally 89.8 km (Casas-Diaz *et al.* 2013) or seasonally migrate over distances from 100 up to 150 km (Singer *et al.* 1981; Jerina *et al.* 2014). Mature, solitary males may move 60 km within a night (Roberts *et al.* 2014). However, Siberia presents larger and more frequent impacts on wildlife mobility at the latitude of our LCPs in comparison with Eastern Europe and Scandinavia, particularly wildfire and logging (Kukavskaya *et al.* 2013). Both may hinder or accelerate eastward movement of wild boar. Those boar staying near their natal home range (Śmietanka *et al.* 2016) traverse only short distances over a relatively long time period (Fig. 3: upper left quarter). Short transmission distances combined with long time intervals (Fig. 3) may also be due to ASFV overwintering in frozen carcasses of wild boar followed by an outbreak in summer. The retention period of infectivity of ASFV in winter-frozen materials of wild boar origin and contaminated soil may persist at least 6 months (Cortiñas Abrahantes*et al.* 2017). This increases the chance of contact by other groups and may explain that in Eastern Europe, where temperatures remain below 0°C for much of the winter, a new, previously unseen epidemiological pattern is unfolding (Beltrán-Alcrudo *et al.*2017). Similar situations may be expected along the LCPs.

The majority of ASF-infected wild boar occurred within a short distance and a short time interval of each other (Fig. 3; Fig. S3, S4). The limited spatial range overlap of wild boar family groups limits transmission of the ASFV between groups by either direct or indirect contact through infected carcasses (Śmietanka *et al.* 2016). However, the frequency of direct contacts between individuals within the family is much higher (FAO 2013; Pepin *et al.* 2016; Podgorski & Smietanka 2018). Nonetheless, ASF has slowly but steadily spread to their neighboring disease-free areas (Podgorski & Smietanka 2018).

Though an instant cross-continental, natural spread of ASF seems unlikely given our findings, the Trans-Siberian Railway and LCP intersections imply a risk of substantially accelerating transmission of ASF by anthropogenic assistance. ASF could be transmitted directly and within several days from west to east across Eurasia by railway transport. In other words, the predicted LCPs may be substituted in stretches by faster anthropogenic pathways.

Although slope hardly contributed to our suitability model, its inclusion in the cost surface instead of elevation resulted in two alternate LCPs from Lake Baikal onward. At the lake, the LCPs reach the highest mountains in its Siberian trajectory. The LCP-elevation avoids primarily higher elevations, resulting in a longer path. The LCP-slope avoids steeper slopes by following small, somewhat elevated valleys and follows a shorter, more direct trajectory to the Impact region.

East of Lake Baikal, our LCPs seem to run through extensive unsuitable areas for ASF-infected wild boar at the small scale (about 1: 4 million) of our maps in this publication. At a more detailed scale, a pattern of small suitable patches becomes apparent. Consequently, multiple transmission paths are possible, but these will bear higher costs and result in a later arrival date.

The Irkutsk ASF case (FAO 2018) of 2017 in domestic pig in Central Siberia at about 1000 km from NE China was not considered as a plausible ASFV source for the Impact region. The Irkutsk and the Shirokaya

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in the Far East of the RF (2019) cases demonstrated that the RF deals competently with ASF.

Though our prediction is based on a set of assumptions and data obtained in Eastern Europe, it has contributed to our understanding of the natural transmission of ASF by wild boar. Our results show that cross-continental transmission of ASF by natural movement of ASF-infected wild boar would take minimally 219 days to arrive at the border of China in the NE and therefore could not be the source of the actual arrival date, 2 August 2018, in NE China.

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COMPETING INTERESTS

The authors declare no competing interests.

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Table 1 The number of ASF-infected wild boar per cover and season in Eastern Europe

Cover *Name shortened*	ASF-infected wild boar/season (No)	ASF-infected wild boar/season (No)	ASF-infected wild boar/season (No)	ASF-infected wild boar/season (No)	Total	Total
	Autumn	Summer	Spring	Winter	No	%
Broadleaved forest >15%	27	53	17	35	132	34.5
Cropland rainfed	20	34	7	13	74	19.4
Mosaic crop/natural	7	28	1	18	54	14.1
Conifer forest >15%	10	17	1	4	32	8.3
Mixed broadleaved/conifer forest	3	14	2	8	27	7.0
Grassland	6	12	1	7	26	6.8
Herbaceous	4	8	-	1	13	3.4
Mixed tree/shrub	2	2	3	1	8	2.1
Various	5	4	2	6	17	4.4
Total/season	84	172	34	93	383	100

Table 2 . Transmission distance (km) and time interval (days) in Eastern Europe

Cover	Season	Distance (km)	Time interval (days)
		Maximum	Minimum
Cropland	Autumn	119.2	4
	Summer	148.3	4
	Spring	113.1	5
	Winter	109.9	4
Forest	Autumn	139.2	4
	Summer	150.0	4
	Spring	100.9	4
	Winter	109.8	4
Grassland	Autumn	90.8	6
	Summer	145.2	4
	Spring	50.4	4
	Winter	60.0	4

Figure 1 Elevation range of ASF-infected wild boar in Eastern Europe. The bars show the frequency of

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ASF-infected wild boar occurrence per elevation class in Eastern Europe. The graph demonstrates that a large majority of ASF-infected wild boar occurred at lowland elevations and only a few were recorded in hills or mountains.

Figure 2 Response curve of ASF-infected wild boar occurrence in Eastern Europe. The curve shows the mean response of replicate runs (red) and its mean standard deviation (blue) in our maximum entropy model (MaxEnt). The graph indicates that the probability of ASF-infected wild boar occurrence decreases as elevation increases.

Figure 3 Scatter plot of ASF transmission distance and time interval by wild boar in Eastern Europe. The plotted points represent the transmission distance and time interval for the ASFV transmission by wild boar as measured in this research based on data from Eastern Europe. There is no relation between distance and time interval. Only in a few cases (lower right corner), the ASFV covered a long distance ($>$100 km) within a short time interval ($<$60 days) or (upper left quarter) a short distance over a relatively long time interval.

Figure 4 Suitability for ASF-infected wild boar across the research area. The map depicts the suitability range for ASF-infected wild boar between the Arctic Circle and the 35° Northern latitude from Eastern Europe across the Eurasian continent to NE China. Red represents the highest and blue the lowest suitability. The highly suitable areas in NW China have been selected as endpoint of the Least Cost Paths for ASFV transmission by infected wild boar.

Figure 5 Least Cost Paths for ASF-infected wild boar to NE China. The map shows the cost surface for ASF-infected wild boar movements. The cost ranges from low (1: dark green) to high (5: white=impermeable). The red dots represent the starting (west) and endpoints (east) of the Least Cost Paths. Both Paths run between 52.5° and 59.5° Northern latitude. The light blue dots represent the ASF-infected wild boar occurrence in Eastern Europe. From Lake Baikal onward, the LCP-elevation follows a northern path along the Lena River and avoids primarily higher elevations, resulting in a longer path. LCP-slope avoids steeper slopes by following small, somewhat elevated valleys and follows a shorter, more direct trajectory to the Impact region. The LCPs starting in Eastern Europe originating from each blue dot run toward the northeast to join and follow the same path and direction after crossing the Ural Mountains.

Figure S1 ASF-infected wild boar occurrence in Eastern Europe per cover. The bars show the occurrence of ASF-infected wild boar per land cover type in Eastern Europe. All forest types (BLF, MF and CF), rainfed cropland (CL) and their mosaics (MC) are showing relatively high occurrences.

Figure S2 The probability of ASF-infected wild boar occurrence in Eastern Europe per cover. The red lines show the probability of ASF-infected wild boar occurrence in Eastern Europe across land cover types as predicted by the maximum entropy algorithm. High probabilities with acceptable SDs (blue lines) are found for the broadleaved (BLF) and conifer (CF) forests, rainfed croplands (CL) and their mosaics (MC). *The contribution of other cover types to the model* is relatively low.

Figure S3 Transmission time interval (days) of ASF-infected wild boar occurrence in Eastern Europe. The bars show the frequency of ASF-infected wild boar occurrence per transmission time interval in Eastern Europe. The graph indicates a large majority of ASF-infected wild boar occurred within a short time interval of each other and only few of them occurred within a long time interval.

Figure S4 Transmission distance (km) for ASF-infected wild boar occurrence in Eastern Europe. The bars show the frequency of ASF-infected wild boar occurrence per transmission distance in Eastern Europe. The graph indicates a large majority of ASF-infected wild boar occurred within a short transmission distance to each other and the frequency of ASF-infected wild boar occurrence decreases as the transmission distance increases, especially at distances $>$ 100 km.

Tables S1 The number of ASF-infected wild boar per cover and per Source region

Source region	Cover	Cover	Cover	Cover	Cover	Cover	Cover	Cover	Cover	Cover	Cover	Cover	Cover
	CL	HB	TS	MC	MV	BLF	BF	CF	MF	MFS	GL	FF	SH

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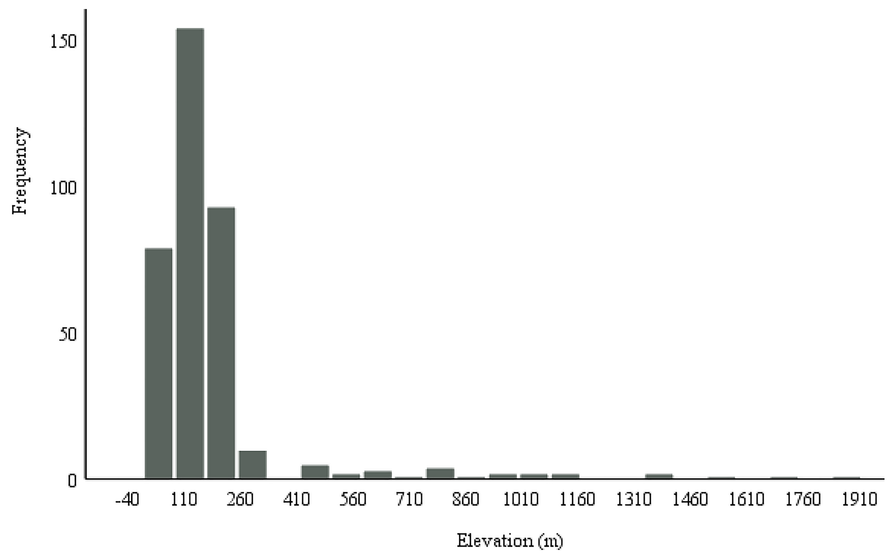
Source region	Cover	Cover	Cover	Cover	Cover	Cover	Cover	Cover	Cover	Cover	Cover	Cover	Cover
Czech RP	3	13	-	9	1	2	-	106	60	13	2	-	-
Estonia	92	37	-	101	14	177	9	172	294	97	29		4
Hungary	23	7	1	1	-	67	-	-	-	3	3	-	-
Latvia	210	77		183	16	519	1	164	337	168	113	-	8
Lithuania	91	42	-	90	1	174	61	-	181	34	6	-	-
Poland	483	366	10	206	22	301	-	590	385	232	179	-	23
Romania	37	15	-	9	-	60	-	-	-	-	3		8
Russia FR	73	13	-	54	7	133	3	32	27	8	19	4	1
Ukraine	22	2	-	2	-	33	-	9	8	2	3	-	1
Total	1034	572	11	655	61	1466	74	1073	1292	557	357	4	45

* For cover description, please refer to Figure S1



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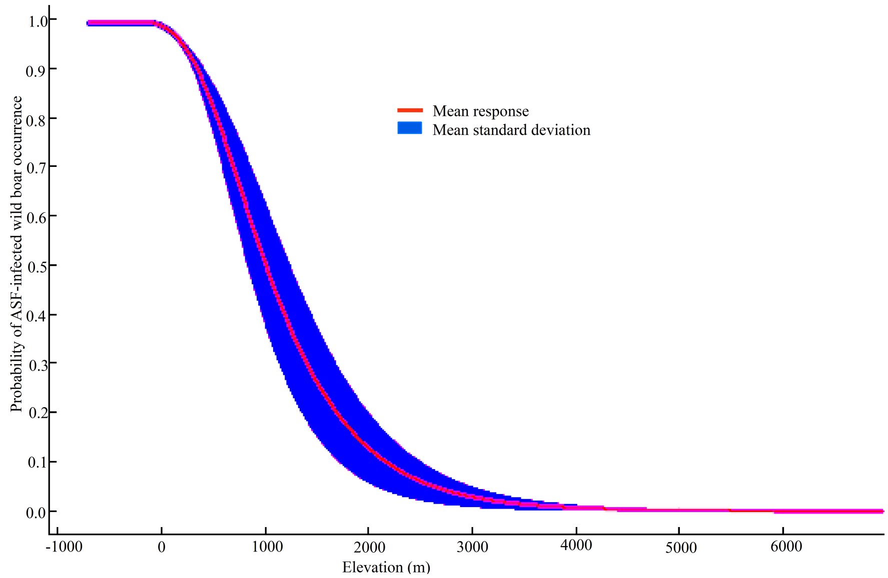

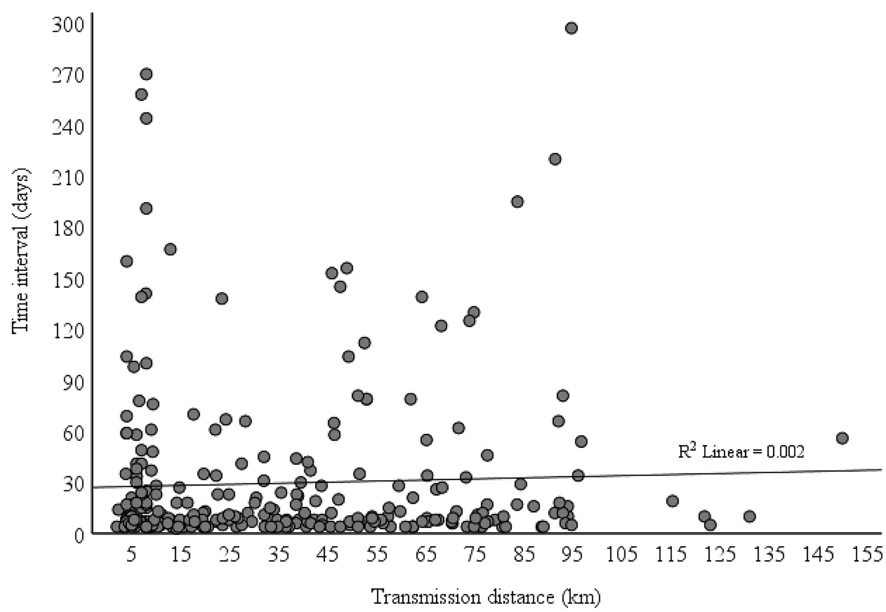

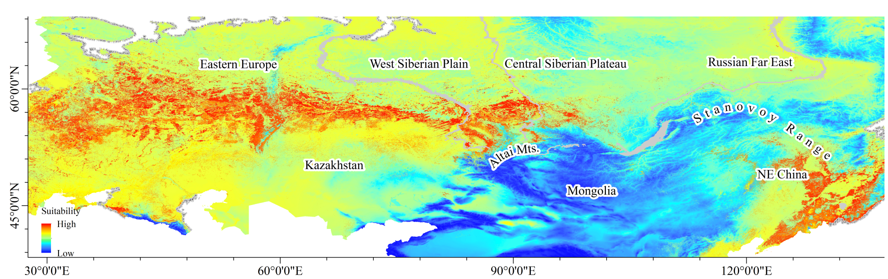

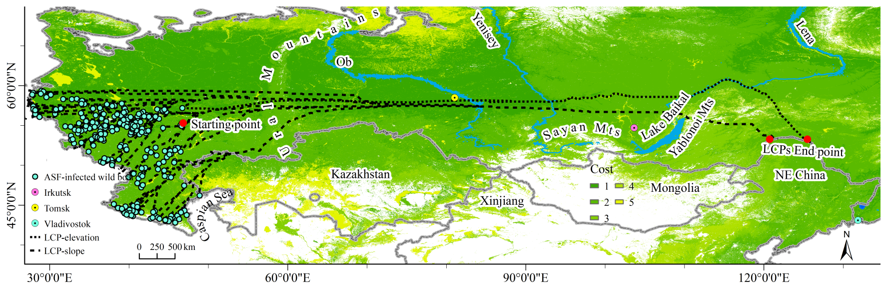

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