HIGH PROBABILITY AREAS FOR ASF INFECTION IN CHINA ALONG THE RUSSIAN AND KOREAN BORDERS

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Summary

African swine fever (ASF) is a transcontinental, contagious, fatal virus disease of pig with devastating socioeconomic impacts. Interaction between infected wild boar and domestic pig may spread the virus. The disease is spreading fast from the west of Eurasia towards ASF-free China. Consequently, prediction of the distribution of ASF along the Sino-Russian-Korean borders is urgent. Our area of interest is Northeast China. The reported ASF-locations in eleven contiguous countries from the Baltic to the Russian Federation were extracted from the archive of the World Organization for Animal Health from July 19, 2007 to March 27, 2017. The locational records of the wild boar were obtained from literature. The environmental predictor variables were downloaded from the WorldClim website. Spatial rarefication and pair-wise geographic distance comparison were applied to minimize spatial autocorrelation of presence points. Principal component analysis (PCA) was used to minimize multi-collinearity among predictor variables. We selected the maximum entropy algorithm for spatial modelling of ASF and wild boar separately, combined the wild boar prediction with the domestic pig census in a single map of suids and overlaid the ASF with the suids map. The accuracy of the models was assessed by the AUC. PCA delivered five components accounting for 95.7% of the variance. Spatial autocorrelation was shown to be insignificant for both ASF and wild boar records. The spatial models showed high mean AUC (0.92 and 0.97) combined with low standard deviations (0.003 and 0.006) for ASF and wild boar respectively. The overlay of the ASF and suids maps suggest that a relatively short sector of the Sino-Russian border has been a high probability entry point of ASF at current conditions. Two sectors of the Sino-Korean border present an elevated risk.

Keywords: African swine fever, climate variables, maximum entropy, spatial modeling, wild boar

1. Introduction

African swine fever (ASF) is a notifiable, highly contagious and fatal viral hemorrhagic fever of all species of the Suidae family. The virus is transmitted by direct or indirect contact with infected suids (Brown & Bevins, 2018). In addition, soft ticks of the genus Ornithodoros serve as reservoirs and vectors (Burrage, 2013; OIE, 2012; Rowlands et al., 2008) and stable flies as mechanical transmitters (Mellor, Kitching, & Wilkinson, 1987; Olesen et al., 2018) of ASFV to suids. Further, ASFV persists in uncooked pig products, facilitating its spread (Murphy et al., 1996). Finally, the virus overwinters in frozen carcasses of wild boar and presumably in frozen pig products (EFSA, 2014). Neither a safe vaccine nor treatment is available for prevention and control (Vergne et al., 2017). ASF has serious socioeconomic impact on international trade in pig and pig products (Bellini, Rutili, & Guberti, 2016; Bosch, Iglesias, Munoz, & de la Torre, 2016).

ASF was first detected in Kenya (Montgomery, 1921) and initially restricted to Africa (Frant, Woźniakowski, & Pejsak, 2017; Murphy et al., 1996) where the virus occurs in an ancient sylvatic cycle with warthog (Bastos et al., 2003). From Africa, ASF has been introduced into other continents (Penrith, 2009). In 1957, the disease spread from Angola to Portugal probably through infected pork fed as swill (Murphy et al., 1996) and from there in 1960 to Spain (Mur, Iscaro, et al., 2017). In the 1960s and 70s, ASF spread to other European countries, Caribbean Islands (Penrith & Vosloob, 2009) and Brazil (Lubisi, Dwarka, Meenowa, & Jaumally, 2009).

In 1985, ASF outbreaks occurred in Belgium and the Netherlands (Vinuela, 1987). In some west European countries, ASF outbreaks were rapidly controlled, but in others, the virus persisted for some time (Bech-Nielsen et al., 1995; Boinas, Hutchings, Dixon, & Wilkinson, 2004; Mannelli et al., 1997). Subsequently, ASFV became widespread in Transcaucasia probably by improper waste disposal from ships at a Black sea port in Georgia in 2007 and from there into the European part of the Russian Federation (RF), most likely through infected wild boar in the same year (Chapman et al., 2011). In Transcaucasia and the RF, both domestic pig and wild boar are affected. In addition to the presence of wild boar, the commonplace backyard swine rearing played a significant role in the wide and fast spread of the ASF in Transcaucasia (Oganesyan et al., 2013). Beyond a suitable wild boar habitat (De la Torre et al., 2013), interaction of infected wild boar with backyard pig farms are considered the main risk factor for the spread of the virus in Eastern Europe (FAO, 2017). Depending on location and scale, the spread of ASF has been associated with a range of environmental variables. These include density of free-ranging pigs, movement of pigs and pig products (Brown & Bevins, 2018), swill-feeding, proximity to slaughter houses and density of rural population (Chenais et al., 2017; Fasina, Lazarus, Spencer, Makinde, & Bastos, 2012; Gornung, Cristaldi, & Castiglia, 2009; Kabuuka et al., 2014; Mur, Atzeni, et al., 2014; Nantima et al., 2015; Penrith & Vosloo, 2009; Randriamparany et al., 2005). Further, pig farm density, piggeries with outdoor feedlots, and high road density have been correlated with the occurrence of ASF outbreaks (Gulenkin et al., 2011; Martínez-lópez, Perez, Feliziani, & Rolesu, 2015). In addition, presence of water bodies has been identified as a risk factor for ASF (Gulenkin, Korennoy, Karaulov, & Dudnikov, 2011; Korennoy et al., 2014). The use of climatic predictors for our large area is justified in the methods section below (2.1), from first principle with reference to the pertinent literature.

Ukraine and Belarus reported ASF in 2012 and 2013 respectively. Several cases of ASF among wild boar and outbreaks among domestic pig were detected during 2015 in the Baltic and neighboring Poland (Sánchez-Cordón, Montoya, Reis, & Dixon, 2018; Śmietanka et al., 2016;

Woźniakowski et al., 2016). From 2007 onward, ASF has been spreading in the RF (Sánchez-Cordón et al., 2018), but not into bordering China. Very recently, an ASF outbreak occurred near Irkutsk, in the RF's Central Asia (Fig 1), posing a risk of ASF introduction into Northern China (Ge et al., 2017). Because China contains almost half of the world's domestic pig population, a major food industry is threatened (Vergne et al., 2017). Consequently, the development of a timely detection and control strategy of ASF has become urgent (Vergne, Gogin, & Pfeiffer, 2015).

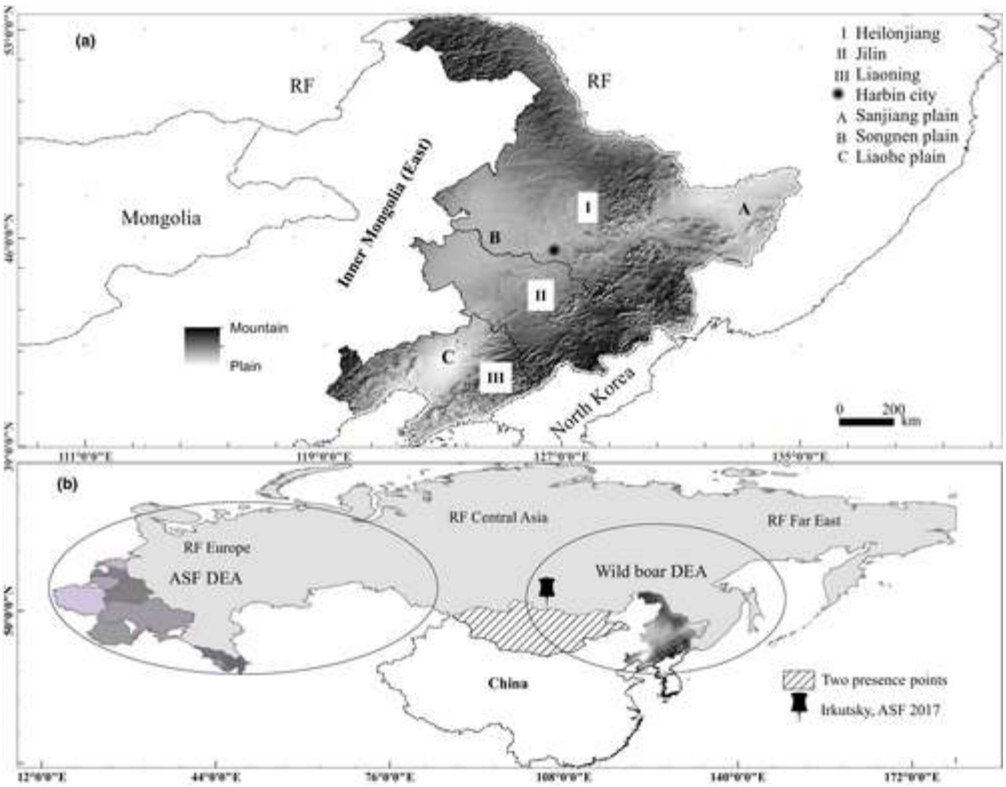

Figure 1. (a). Location Map of the three provinces (I, II and III) in Northeast China (AOI). (b). DEA for ASF (right) and wild boar (left). From Mongolia only two presence points of wild boar were available

ASF has been established and maintained in Sardinia for nearly four decades (Mur, Iscaro, et al., 2017) through direct contact between domestic pig and wild boar (Ravaomanana et al., 2011). Due to the presence of non-registered domestic pigs (known as brado), wild boar, and low-biosecurity pig farms) in Sardinia, ASFV became established and small outbreaks spread mainly by fomites (e.g. cloths; car) between small piggeries (Mur, Sánchez-Vizcaíno, et al., 2017). The role of the wild boar in ASF epidemiology, and more specifically their capacity to maintain the disease, is controversial. Wild boar seems unable to maintain the disease without any other source of infection (Laddomada et al., 1994; Mur et al., 2012; Rolesu et al., 2007). However, in some east European countries (Belarus, RF and Ukraine), ASF has crossed national borders through infected wild boar (EFSA, 2014) resulting in large epidemics both in domestic pig and wild boar (Gallardo et al., 2015). In summary, infected wild boar populations present a constant risk for domestic pig and vice versa (Sánchez-Vizcaíno, Mur, & Martínez-López, 2012).

Pig farming in China is carried out in backyards, small, and large farms. However, the percentage of pigs that are raised in large intensive pig farms in China is rising quickly (McOrist, Khampee, & Guo, 2011). After the agricultural reform in the late 1970s, some backyard producers expanded their farm sizes and became specialized small piggeries. At the same time, most backyard pig producers gradually abandoned farming (Chen & Wang, 2013). According to industry reports, the number of backyard pig producers has declined consistently since the mid-2000s. About 80% of the rural households in China do not raise pigs (Gale, Marti, & Hu, 2012; Qiao, Huang, Wang, Liu, & Lohmar, 2016). Free ranging pigs are unknown in our AOI.

The Eurasian wild boar is expanding its range while growing in numbers (Bosch, Rodríguez, et al., 2016; Oliver & Leus, 2008; Russo, Massei, & Genov, 1997; Segura, Acevedo, Rodriguez, Naves, & Obeso, 2014). Several policies are conducive, purposely or unintentionally for an ongoing spread and higher densities of wild boar in the area of interest (AOI). Since the 1990s, marginal mountainous farmlands and settlements are abandoned and spontaneously rewilding in Northeast China and the bordering RF. The rewilding process is reducing contacts between domestic pig and wild boar (Liu, Wang, Gao, & Deng, 2005; Vergne et al., 2017). Additionally, new nature reserves have been established in Northeast China. Further, China has legislated a protected status of wild boar (He, 2014; Li, 2013). These trends brings about health risks because wild boar is a potential host for numerous pathogens (Acevedo, Quirós-Fernández, Casal, & Vicente, 2014) including ASF (Mur, Martínez-López, et al., 2014).

Climate may affect wild boar dynamics through spring and summer temperatures affecting food supply (Acevedo, Escudero, Muñoz, & Gortázar, 2006), especially fruit, seed and nut bearing trees and shrubs (Vetter, Ruf, Bieber, & Arnold, 2015). At the RF side of the Sino-Russian border recent (2000-2016) deforestation has been observed (Hansen et al., 2013), largely due to wildfire (Cahoon, Stocks, Levine, Cofer, & Pierson, 1994; Vivchar, 2011). Wildfires and the resulting deforestation may drive populations of wild boar to migration (Olival, 2016). The risk of introduction of ASF by wild boar into EU countries has been assessed (Bosch, Rodríguez, et al., 2016; Bosch, Iglesias, et al., 2016). However, little is known on the geographic distribution and suitable environments for ASF and wild boar in Northeast China. For a wild boar management framework and an epidemiological control of the ASFV, reliable predictions of wild boar and disease distribution are highly desirable.

We selected the maximum entropy algorithm (MaxEnt) from the large number of predictive species distribution models (SDMs). MaxEnt is an empirical, deterministic, non-parametric, pixel-based, machine-learning method for presence-only point data analysis. It calculates probabilities of species presence without assumptions about the distribution of either species or predictors. In addition, MaxEnt generates response curves of each continuous predictor essential in interpreting model performance (Gils, Conti, Ciaschetti, & Westinga, 2012; Gils, Westinga, Carafa, Antonucci, & Ciaschetti, 2014). MaxEnt has become the SDM tool of choice for animal distribution studies, including wild boar (Bosch, Mardones, Pérez, Torre, & Muñoz, 2014), bear (Gils et al., 2014) and anthrax (Abdrakhmanov et al., 2017). Furthermore, MaxEnt provided a robust response independently of a number of selected variables of 5 or lower (Gils et al., 2014; Navarro-Cerrillo, Hernández-Bermejo, & Hernández-Clemente, 2011). Early MaxEnt studies did neither consider spatial autocorrelation of presence point data nor multi-collinearity of environmental predictor variables. In addition, early users reported that MaxEnt modelling was neither sensitive to spatial autocorrelation (Cheng, 2008) nor collinearity issues (Elith et al., 2011). Subsequently, other case studies came to contrarian conclusions (Anderson & Gonzalez, 2011; Boria, Olson, Goodman, & Anderson, 2014; Duque-Lazo, 2013; Kramer-Schadt et al., 2013; Varela, Anderson, García-Valdés, & Fernández-

González, 2014; Veloz, 2009). In hindsight, disregard of multi-collinearity is difficult to understand as climatic variables are known to be highly correlated. Therefore, we may assume that the number of predictor variables (n=8-40) used in the early days of spatial modelling (Franklin, 2009) contained correlated variables.

Mullins et al., (2013) used an algorithm (GARP) less predictive compared to MaxEnt (Elith et al., 2006; Padalia, Srivastava, & Kushwaha, 2014; Phillips, Anderson, & Schapire, 2006). Further, MaxEnt has a proven record of transferability between regions (Duque-Lazo, Gils, Groen, & Navarro-Cerrillo, 2016; Heikkinen, Marmion, & Luoto, 2012). In addition, our selection and reduction of the number of predictor variables by PCA and response curve SD from a large set of options was explicitly geared at achieving the optimal transferability from the current distribution area to another geographic area.

2. Materials and methods

2.1. Research area and data

Our area of interest (AOI) are the Heilongjiang, Jilin and Liaoning provinces in Northeast China located between N 38°43′-53°23′, E 118°37′-135°05′ in the center of Northeastern Asia (Fig 1). The three provinces together cover 78.7 $\times 10^4$ km^2, mostly forested mountains and nearly 30% farmed intermountain and river plains. The natural forest are classified from north to southwest as deciduous coniferous (larch), coniferous and mixed red pine/broad-leaved deciduous and deciduous broad-leaved (oak). The three plains consist of fertile phaeozem/chernozem (dark/black soil) (IUSS Working Group WRB, 2007, 2014) and are cultivated for soybean, maize and japonica rice. The AOI climate is characterized by short, warm and semi-dry to humid summer seasons alternating with long, frosty and dry winters. The annual precipitation increases from 400 mm at the Inner Mongolian side in the northwest to 1000 mm at the Yellow Sea coast in the south. The number of frost days ranges from about 100-200. The AOI shares a 4300 km border with the Far East of the RF, mostly following rivers (Argun, Amur and Ussuri) and a 1420 km border with North Korea also following rivers (Yalu and Tumen). In addition, the Xingan Mountains run parallel to the border of Heilongjiang and the RF in the north down to 48° N and the Changbai Mountains parallel to the eastern section of the Sino-Korean border. South of 48° N, the Sino-Russian border runs through the farmed Sanjiang plain. Farming is evident at both sides of the Northeast China and Korean borders and likely to include piggeries and/or backyard pig breeding. These long borders may present a challenge to the prevention of ASFV-infected wild boar entering China. The rivers constituting the borders can be crossed by wild boar in the summer by swimming and in the winter by walking over the ice.

Northeast China has the highest endowment of cropland per capita (USDA, 2014) and 10% of the pigs in China (46.10^6) (http://kids.fao.org/glipha; http://www.stats.gov.cn), (Figure S1C). The pig farming/ production depends on an abundant supply of feed: maize and soybeans (Chen & Wang, 2013). The data extraction area (DEA) for ASF records from the World organization for animal health (OIE) (www.oie.int) consists of the eleven contiguous countries from the Baltic to the Far East of the RF (Table 1) containing geographic coordinates as available from July 19, 2007 to March 27, 2017 (Fig 1B). The OIE records in the DEA include both infected wild boar and infected domestic pigs (n=4462) (Table 1). Two wild boar subspecies *Sus scrofa sibiricus* Staffe, 1922 and *Sus scrofa ussuricus* Heude, 1888 are common in Northeast China (Gao, Zhang, & Hu, 1995), bordering Far East of the RF and Mongolia (Oliver & Leus, 2008; www.planet-mammiferes.org). The DEA for the two wild boar subspecies contains the Eastern portion of the ASF DEA (Fig 1B). We extracted most wild boar presence points from published literature (n=135) (Gao et al., 1995; Jiang et al., 2006; Li et al., 2010; Li et al., 2010; Ma & Liu, 2012; Meng et al., 2013; Ramayo et al., 2010; Wang et al., 2008; Wang, Ma, Li & Wang, 2005; Xu, Cai, Ju & Zhao, 2011; Yu, Wu & Fan, 2009; Zhang, Liu & Liu, 2015; Zhou et al., 2010; Zhu et al., 2011). In addition, we extracted a few records (n=4) from the Global Biodiversity Information Facility. (GBIF.org, 2016) .

Table 1. Disease (ASF) and host (wild boar), species presence records and prediction areas of two wild boar subspecies: *Sus scrofa sibiricus* Staffe, 1922 and *Sus scrofa ussuricus* Heude, 1888.

	ASF	Wild boar
Presence points	2005-2017	1984-2015
Admin area	Baltic†; Poland; Belarus; Ukraine; Romania; Transcausia‡; RF;	RF Trans-Ural; NE China; Mongolia ††
DEA	Around presence points	Around presence points
No of records	4462	139
Selected records	1184	84
Source	www.oie.int	www.gbif.org

†Estonia, Latvia and Lithuania; ‡Georgia, Armenia and Azerbaijan;

†† Mongolia =2 presence points

We extracted climatic predictor variables from the WorldClim version 1.4 (2016) with data from 1950 – 2000 at 30 arc-second resolution (www.worldclim.org). This fine spatial resolution is necessary to capture environmental variability that may be lost at coarser resolutions, particularly in the mountainous areas (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). We extracted the following climate variables: monthly precipitation (n=12), monthly mean, minimum and maximum temperature (n=36), derived bioclimatic variables (n=19) and elevation (Table S3). Different environmental variables (and time scales) may operate at each hierarchical level (Wiens, 1989). At the highest hierarchical level, that is large areas, climate is the dominant environmental variable in SDM (Pearson, Dawson, & Liu, 2004). Further, the pertinent literature contains abundantly cited articles using exclusively climatic predictors for species distributions over large areas with the MaxEnt algorithm (Elith et al., 2011; Franklin, 2009; Giles et al., 2014; Rödder et al., 2009; Sobek-Swant, Kluza, Cuddington, & Lyons, 2012; Veloz, 2009), presumably fully aware of the hierarchy theory and that over smaller areas additional predictors would be required (Allen & Starr, 1982). In addition, our exclusive use of climatic predictors follows from ecosystem theory. At the scales of our research, climate is not only a direct but also an indirect predictor of species distribution acting, among others through vegetation cover, forest type, human population density and animal food resources (Guisan & Zimmermann, 2000). To minimize potential spatial autocorrelation of presence points, and multi-collinearity of variables, we preprocessed the presence points and the environmental predictor variables. We used spatial rarefication, also known as (aka) filtering to minimize spatial autocorrelation (aka pseudo-replication) and Principle Component Analysis (PCA) to reduce the number of correlated variables (aka dimensionality). The latter because PCA does not compromise the original relationship between the variables and resulted in PCs that constitute orthogonal projections of the transformed variables (Robertson, Caithness, & Villet, 2001).

2.2. Preprocessing of spatial modelling data

To minimize spatial autocorrelation (Mark & Fortin, 2002), we filtered the presence point records using the SDM Toolbox v1.1c (Brown, 2014) integrated into ArcGIS 10.3. We entered ASF and wild boar records using the default setting that is natural break with a maximum distance of 25 km and a minimum of 5 km for the first step of the analysis. For the second step, spatial rarefying, we set a minimum distance of 10 km between each pair of presence point records (Anderson & Raza, 2010; Radosavljevic & Anderson, 2014). For computation of all pair-wise distances between each ASF and wild boar records, we used the geographic distance matrix generator v1.2.3, a platform-independent Java application that implements the same suite of spherical functions as the perpendicular distance calculator (Ersts, 2017).

To minimize multi-collinearity of environmental predictor variables, a PCA was carried out (Cruz-Cárdenas, López-Mata, Villaseñor, & Ortiz, 2014; Moriguchi, Onuma, & Goka, 2016) using SPSS 22.0. We used eigenvalues larger than 1.0 and the scree plot criterion or 'broken stick' stopping rule for PCA in item level factoring (Bernstein, Garbin, & Teng, 1988). Suppression of unnecessary loading and rotation of factor pattern of climatic variables (Landau & Everitt, 2004) were used to retain climatic predictor variables for subsequent analysis in MaxEnt.

2.3. Spatial models of ASF and wild boar

For ASF and wild boar, we developed spatial models separately and transferred these to the AOI. MaxEnt version 3.4.1 (Phillips, Anderson, Dudík, Schapire, & Blair, 2017) was used to build and calibrate the spatial models based on 10 fold cross-validated using a regularization multiplier (β=2) (Elith, Kearney, & Phillips, 2010; Radosavljevic & Anderson, 2014) and linear and quadratic features only because the two features consistently perform better and produce smooth models (Anderson & Gonzalez, 2011; Elith et al., 2010). Mateo-Tomás, Olea, Sánchez-Barbudo, & Mateo (2012) calculated Pearson's pair-wise correlations of the predictions of the models (i.e. habitat suitability values) obtained from the 10 fold cross-validated models. Instead, we have used an equivalent cross-validation method (Khanum, Mumtaz, & Kumar, 2013). Models built using the default regularization (β=1) may produce predictions concentrated in a much narrower geographic area. However, variable selection may have a larger effect than changing the regularization parameter (Warren, Wright, Seifert, & Shaffer, 2014). Reduction of the number of predictor variables (Tuanmu et al., 2011) is likely to improve model performance (Feilhauer, Somers, & van der Linden, 2017; Skowronek et al., 2018) and increase model transferability (Duque-Lazo, 2013). We divided the selected presence records into 75% training and 25% testing portions. For the remaining parameters, we kept the MaxEnt default settings. The area under the receiver operating characteristic (ROC) curve (AUC) as embedded in the MaxEnt was used to assess the goodness-of-fit of the model. In addition, the Jackknife test and the variable response curves were selected to identify the relative contribution of predictor variables to the model (Elith et al., 2011; Korennoy et al., 2014). All predictor variables with factor loading $\geq$ 0.9 during PCA were added to the model (Tables S1, S2). Next, the least contributing predictors of the non-collinear variables were eliminated stepwise until each variables contribute more than 10% to the model in MaxEnt (Elith & Leathwick, 2009; Gils et al., 2014). Finally, we eliminated predictor variables with a high standard deviation (SD) (Duque-Lazo, Navarro-Cerrillo, Gils, & Groen, 2018) based on visual observation of the response curves. Lastly, both prediction maps and the domestic pig distribution map were smoothed by taking the average probability value for each three-by-three pixel neighborhood (Gils et al., 2014). The domestic pig distribution map was resampled to harmonize the resolution and cell value range with the wild boar prediction map and reclassified using the SDM toolbox. Then we combined the smoothed wild boar prediction map and the actual domestic pig distribution map using the ArcGIS Spatial Analyst/Fuzzy overlay tool (OR option). Subsequently, the AND option was used to overlay the smoothed ASF prediction map with the output of the two maps that returns the least common denominator with a probability ≥0.5 to be suitable for ASF and the combined wild boar and pig distribution areas.

3. Results

3.1. Presence record filtering and predictor variables selection

The filtering process resulted in the selection of 1184 ASF and 82 wild boar records (Table 1). The pair wise distances between records was larger than 9.8 km. The PCA delivered five PCs together accounting for 95.7% of the total variance (Table 2; Fig 2). After exclusion of unnecessary factor loading, four PCs and thirty-three predictor variables were retained. Subsequently, the PCs were labeled as long cold winter, short hot summer, low winter precipitation and high summer precipitation respectively (Table S1). The four PCs were uncorrelated |r|< 0.7 and selected to run the SDM. After stepwise removal, only the minimum temperature of March and the maximum temperature of May for ASF as well as the minimum temperature of August and maximum temperature of May for wild boar were included to run the final SDM (Table 3; Table S2).

Table 2: PCA of climatic predictors

	Initial Eigenvalues		
CP	**Total**	**Variance %**	**Cumulative %**
1	34.4	50.7	50.7
2	18. 9	27.8	78.5
3	5.8	8.5	87.0
4	4.3	6.4	93.4
5	1.6	2.3	95.7

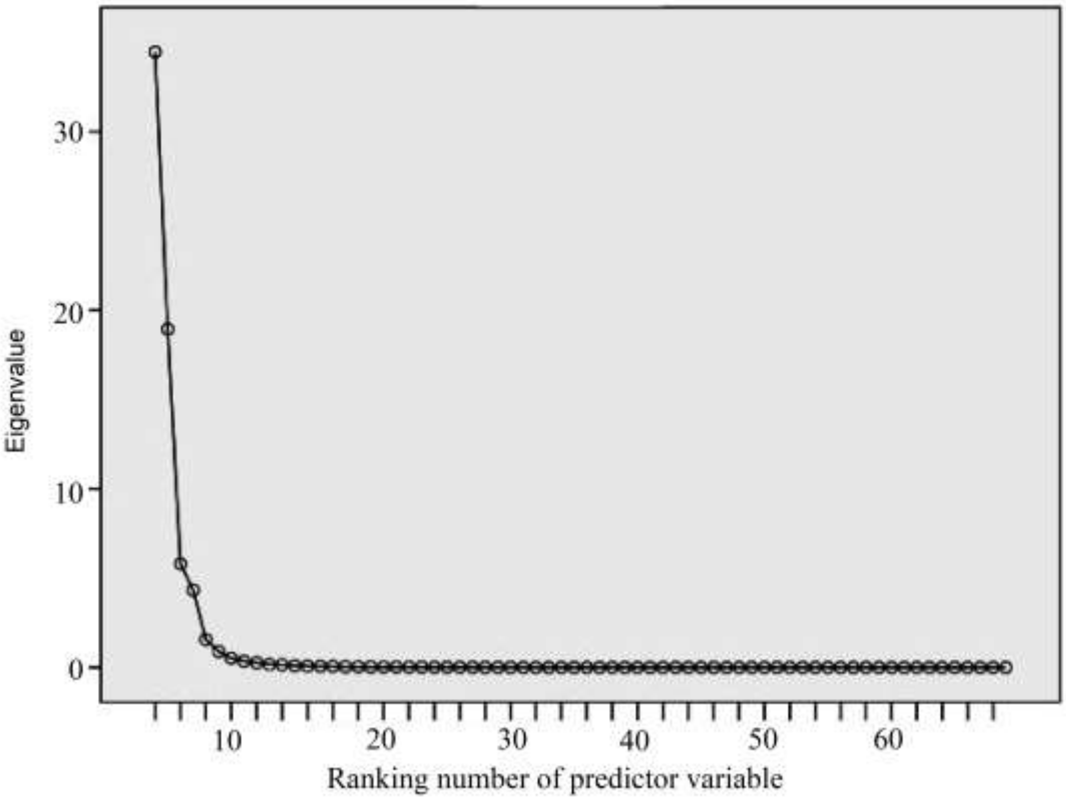

Figure 2: Scree plot of predictor variable factor loading in descending order.

Table 3: Estimates of relative contributions of the environmental predictor variables to the final models. T=temperature; Min=minimum; Max=maximum

ASF			Wild boar		
Variable	**Contribution %**	**Permutation importance**	**Variable**	**Contribution %**	**Permutation importance**
Min T Mar	87.4	83.7	Max T May	64.9	62.1
Max T May	12.6	16.3	Min T Aug	23.8	37.9

3.2. Spatial models for ASF and wild boar

The average output result of the 10 fold cross-validation of the ASF SDM shows high training and test AUC values combined with low standard deviations (0.92; 0.003). The bell-shaped response curves, both normal/Gaussian distributions indicated that the probability of ASF occurrence is highest around -10 to zero °C minimum temperature of March (light late winder frost) and + 5 and 15°C maximum temperature of May (early spring temperature) (Fig 3A). The predicted climatic suitability for ASF covers a major portion of the Liaoning province in the south of the AOI and decreases from the Jilin to the Heilongjiang province towards the north (Figure S1A).

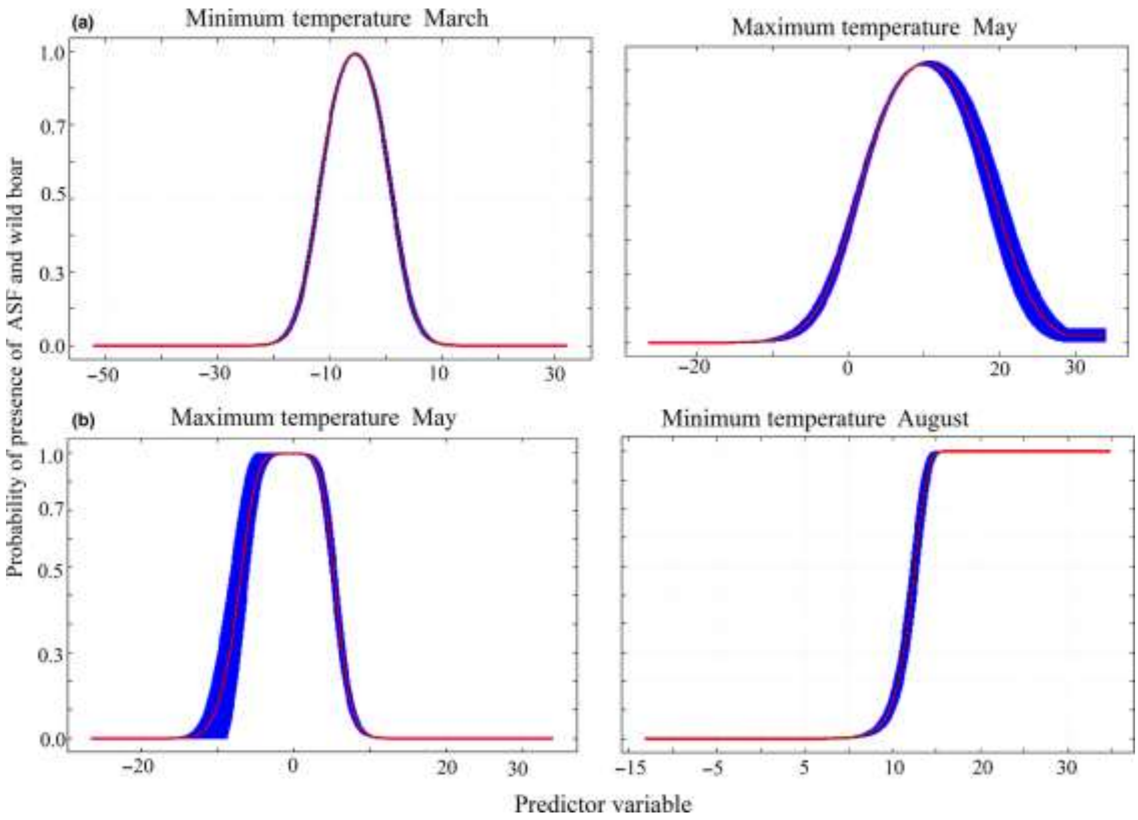

Figure 3: Response curves for ASF (A) and wild boar (B). The curves show the mean response (red) and the mean standard deviation (blue).

The average output result of the 10 fold cross-validation training and test AUC values for the wild boar SDM are high with low standard deviations (0.97; 0.006). The bell-shaped response curves assert that the probability of presence of wild boar was high with a maximum temperature of May around the freezing point and declining rapidly above and below this point. The probability of wild boar presence is zero until 7℃ minimum temperature in August and increases sharply from zero between 7 and 10℃ until remains high thereafter (Fig 4B*)*. Finally, the ASF and wild boar model share the maximum May temperature as predictor variable, although with different values. The ASF with an optimum around 10°C and wild boar around freezing point.

A contiguous low probability for both virus and host is predicted in the Xingan Mountains to the north of about 48° N and in the Liao river plain in the extreme west of the AOI. A high probability is predicted in two disjunctive larger patches and a small one in between, all three south of 48° N. The largest patch (34 %) is located in the southwest, bordering Korea; the smaller (1.8%) in the east bordering the RF and the smallest (1%) in the middle also along the Korean border. The large patch consists of the Changbai Mountains along the Korean border, the Liao river plain and the Songnen intermountain plain in the center of the AOI. The eastern patch is situated in the Sanjiang plain along the river Ussuri and through the Khanka Lake (Fig 3). About a third of the southeastern border between China and Korea (420 km), mainly in the Liaoning province along the river Yalu and Tumen is situated in the high probability zone for virus and host. In the central section of the Sino-Korean border in the Changbai Mountains, a small stretch (154 km) in the Jilin province is also crossing a high probability area. Further, a small southern section of the Sino-Russian border in Heilongjiang province along the river Ussuri (327 out of 937 km) is also highly suitable for both disease and host (Fig 4).

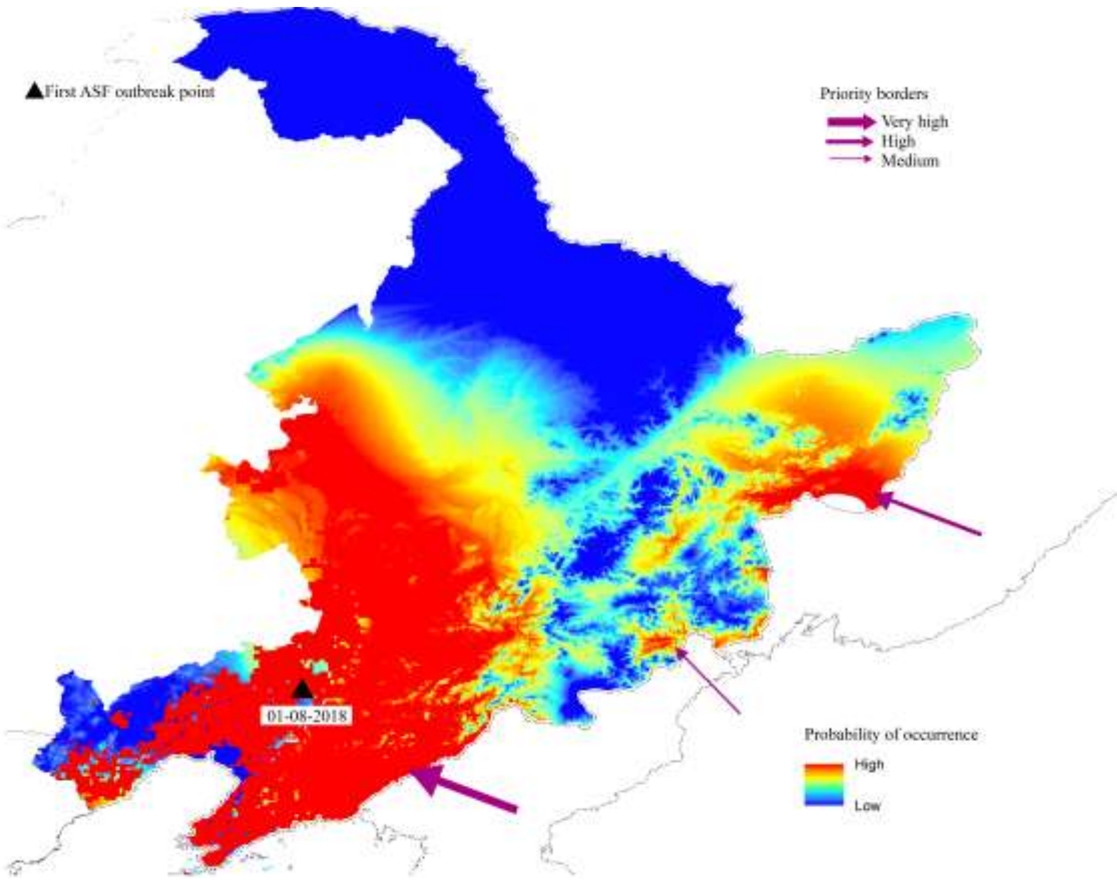

Figure 3: Probability of occurrence of ASF and the host with the high-risk sectors of the international borders.

4. Discussion

The filtering of presence records to minimize their spatial autocorrelation, retains a substantial number of ASF records (>1000) and a relatively low, but optimal number of wild boar records for the MaxEnt algorithm (Gils et al., 2014; Hernández, Graham, Master, & Albert, 2006; Wisz et al., 2008). The filtering of the environmental predictor variables to minimize multi-collinearity, delivers three classical meteorological rather than bioclimatic variables. This finding suggest that the standard practice of using exclusively one type of climatic variables, may fail to identify effective climatic predictors. The selected variables represent monthly minimum or maximum temperatures during spring or summer rather than annual, seasonal, average, precipitation or winter values. The emergence of the maximum spring temperature from a set of climatic variables as the best predictor in a spatial model was also reported by Li et al. (2017). These findings suggest, to include monthly minimum and maximum spring temperatures as predictor variables in SDMs.

Our ASF and wild boar models, each with two predictors show a high AUC value. This corroborates that predictor variables appropriately filtered from a large set of variables may produce good predictions (Duque-Lazo et al., 2018; Gils et al., 2012; Varela et al., 2014). We pioneered combining non-spatial (PCA), spatial (backwards stepwise elimination and SD of the response curve) filtering methods of environmental variables with success, suggesting that both may be used to complement each other. The response curves for the ASF and wild boar models are smoothly bell-shaped with low SD suggesting a good transferability of the model (Duque-Lazo, 2013). Our setting of the MaxEnt algorithm for linear and quadratic features only, instead of the default of five, may have contributed to the smooth curves (Elith et al., 2010), but smooth curves may be also achieved at the default setting (Duque-Lazo et al., 2018).

The highest probability of occurrence of ASF is at a minimum monthly temperature in early spring below zero °C. The frosty spring may allow the persistence of ASFV infectivity. This is corroborated by the findings that infectious ASFV in excrement and meat shows a higher survival (Beltrán-Alcrudo, Arias, Gallardo, Kramer, & Penrith, 2017; EFSA, 2014). The response of the second predictor of ASF, a late spring maximum temperature between +5 and 15°C may imply that the infectivity of ASFV in winter-frozen materials of wild boar origin, including feces and putrefied blood may persist at least until May (EFSA, 2014). In parts of Eastern Europe, where temperatures also remain below 0°C for much of the winter, a new, previously unseen epidemiological pattern is unfolding with most cases detected in the summer months and the presence of the infective virus in carcasses in fields or forests until the spring (Beltrán-Alcrudo et al., 2017). During the hot summers the infectivity of the ASFV will be destroyed (Murphy et al., 1996).

The probability of presence of wild boar was high at early spring temperatures around freezing point. Our finding is in agreement with the observation that temperatures below - 15°C are limiting for piglets, even although they spend several days in the nest (Baskin & Danell, 2003). In addition, the probability of wild boar presence is zero until the 7°C for the minimum temperature during summer. The probability increases sharply from zero upwards and remains high above values 10°C. The 7°C is the physiological threshold for plant growth and obviously, wild boar requires a plant growing season for food. Among ungulates, wild boar exhibits strong responses to food pulses and prefers high energy food, including maize and nuts as well as cover for protection against predators (Bisi et al., 2018; Massei & Genov, 2004). Our findings suggest that if ASFV would spread into North Korea, a very high priority for customs, veterinary inspections and facilities as well as wild boar management for the western sector of the Sino-Korean border would be required (Fig 3). This very high priortiy border runs along the river Yalu, Tumen and its tributaries with farmland and forested mountains at both sides. The high priority section of the Sino-Russian border centered on the Khanka Lake consists of farmland interrupted by patches of forested mountains at both sides of the border. Both high-risk border sections are located in water bodies, river or lake. The presence of wild boar along the rivers contributed to ASF introduction into the European part of the RF from Transcaucasia (Gogin, Gerasimov, Malogolovkin, & Kolbasov, 2013).

An additional risk is presented by the relative proximity of international sea ports, Vladivostok's (Russia) and Dalian (China), each about 250 km to the nearest high risk border section. The ASFV outbreaks elsewhere (Portugal; Georgia) have been associated with infected cargo and waste of ships (Chapman et al., 2011; Murphy et al., 1996). Further, the area both sides of the high risk sections of the borders is farmed and likely to include piggeries and/or backyard pig breeding.

Mating contact of free-ranging wild boar and breeding wild boar in ranches may lead to disease transmission. Subsequently, personnel of wild boar ranches may transmit ASF to low biosecurity piggeries in the farmed plains. If valid, that could set the stage for follow-up studies and targeted control measures, for example, wild boar proof fencing and disinfecting procedures at ranch entry and exit points.

We suggest a detailed follow-up study along the identified priority section of the Sino-Russian and Sino-Korean borders. The study should include wild boar distribution and movement, farmland abandonment, wildfire hazards, road transport network, location of piggeries and backyard pig breeding. When the need arise, an integrated spatial information system will facilitate locating quarantine and other veterinary facilities, wild boar proof fences, wild boar population control, prohibition and development zones for piggeries, routing alternatives for meat products, waste and life animals.

Just 30 days after the submission of our manuscript to this Journal at 02-07-2018, the first ASF infection in China was reported by the OIE at 01-08-2018 within the high probability area in Northwest China (Fig 3).

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Conflict of Interest Statement

The authors declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Author Contributions:

Wang Xiaolong conceived the study, supervised and edited the manuscript. Fekede Regassa Joka and Van Gils Hein contributed to the data filtering, analysis, interpretation, discussion, manuscript writing and map design. Huang LiYa contributed to the conception of the study and expertise on wild boar in Northeast China. The four authors contributed each significantly and participated sufficiently in the research to be accountable for all aspects of the manuscript.

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Supplementary Material

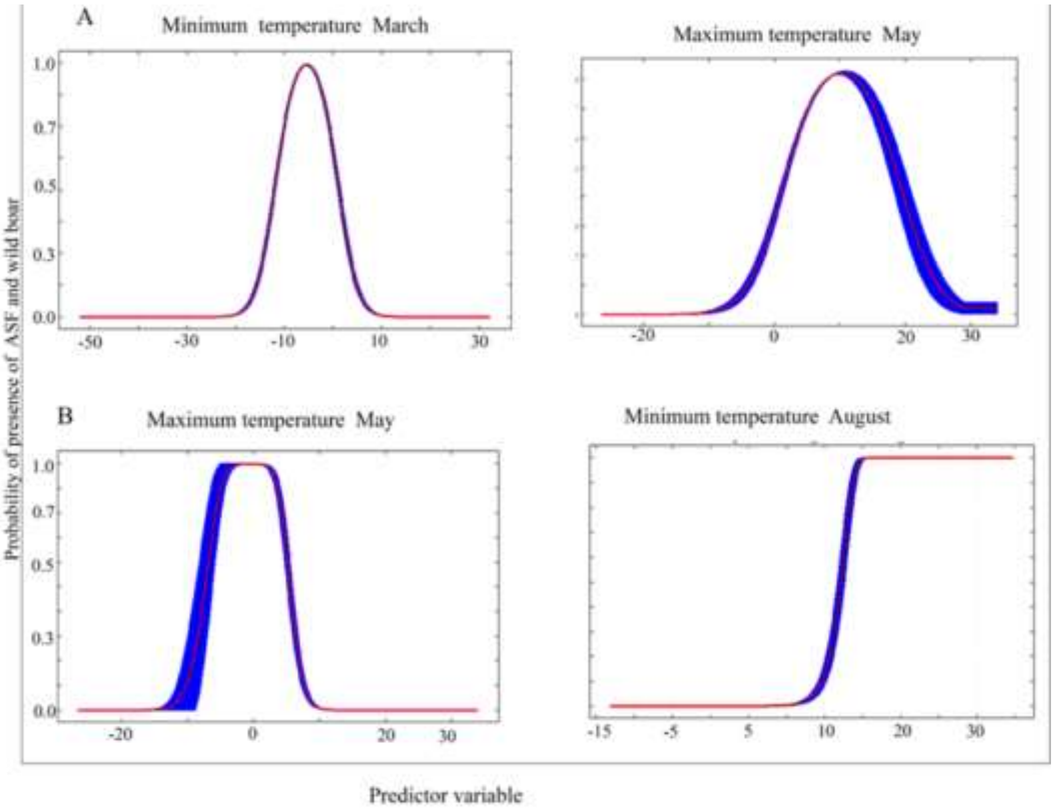

Figure S1: Probability of presence of ASF (A), wild boar (B), Domestic pig distribution (C) overlay of wild boar with actual Domestic pig distribution (D). †Source (C): http://www.fao.org/geonetwork/srv/en/, (FAO, 2007)

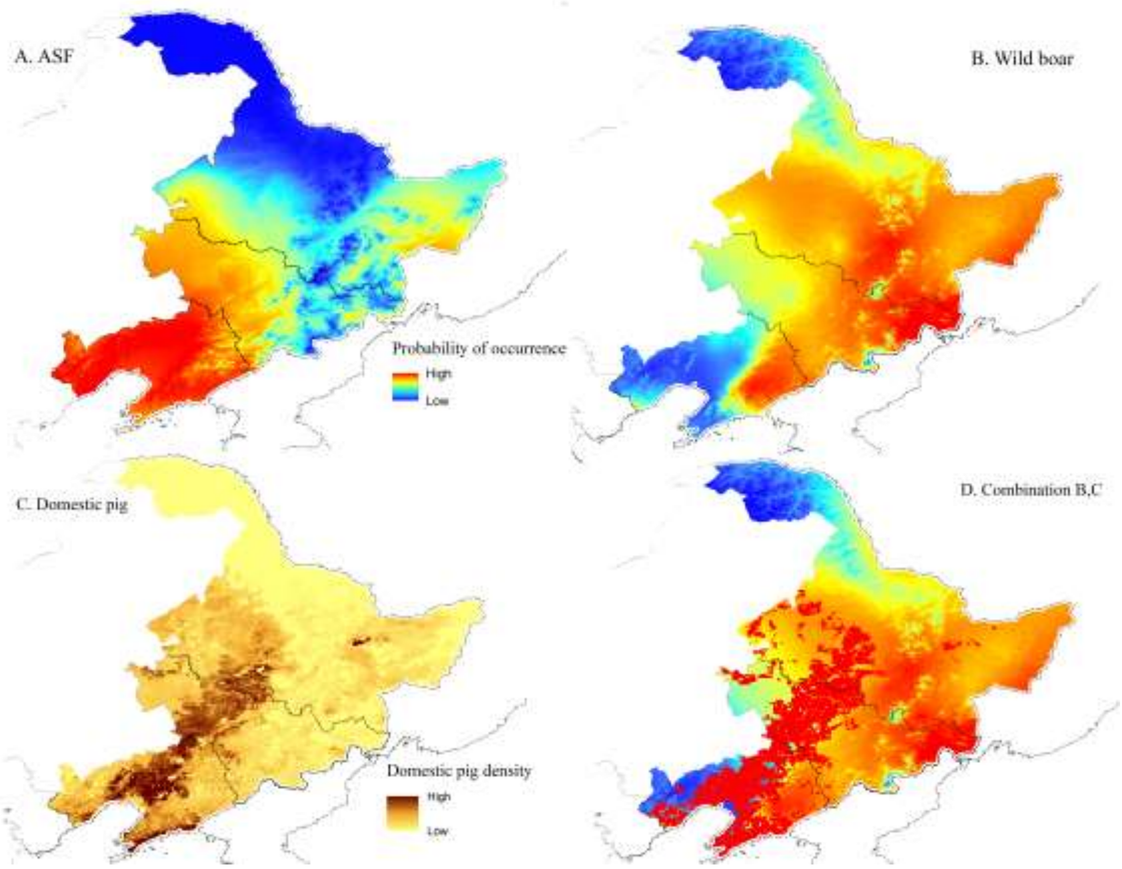

Figure S2: Predictor variables and factor loading as selected by the PCA

Table S1: Predictor variables and factor loading as selected by the PCA

Predictor variable	Component				Label
	1	2	3	4	
Min T Feb	.93				
Mean T Jan	.94				
Mean T Feb	.94				
Mean T of Coldest Quarter	.94				
Min T of Coldest Month	.93				
Min T f Jan	.93				
Min T Nov	.93				Long cold winters
Mean T Dec	.92				
Max T Jan	.92				
Min T of Dec	.91				
Mean T of Nov	.91				
Min T March	.91				
Max T Dec	.90				
Mean T of Jul		.99			
Mean T of Warmest Quarter		.98			
Max T of Warmest Month		.97			
Max T of Jul		.97			
Mean T Aug		.97			
Max T June		.96			
Max T Aug		.96			Short hot summers
Min T Jul		.96			
Mean T of Jun		.96			
Max T May		.94			
Min T Aug		.93			
Min T Jun		.90			

Mean T May	.90			
P Jan		.92		
P of Coldest Quarter		.91		Low winter precipitation
P December		.91		
P of Warmest Quarter			.95	
P of Wettest Month			.94	High summer precipitation
P of Wettest Quarter			.94	
P Aug			.93	
Elevation			.92	Elevation

Table S2: Descriptive statistics of the predictor variables used to run the final model

Predictors ℃	**Min**	**Max**	**Mean**	**SD**
Min T Aug	0	19.5	12.8	2.6
Min T Mar	-29.1	5.0	-5.8	3.5
Max T May	0	25.5	18.6	2.9

Table S3: List of raster data downloaded from the WorldClim database

	Predictor variables	Unit
1	Annual mean temperature	℃
2	Mean diurnal range (Mean of monthly (max temp - min temp))	
3	Isothermality (Mean diurnal range/T annual range) (*100)	
4	Temperature seasonality (standard deviation*100)	
5	Max temperature of warmest month	
6	Min temperature of coldest month	
7	Temperature annual range (Max TWM-Min TCM)	
8	Mean temperature of wettest quarter	
9	Mean temperature of driest quarter	
10	Mean temperature of warmest quarter	
11	Mean temperature of coldest quarter	
12	Annual precipitation	
13	Precipitation of wettest month	
14	Precipitation of driest month	
15	Precipitation seasonality (Coefficient of Variation)	
16	Precipitation of wettest quarter	
17	Precipitation of driest quarter	
18	Precipitation of warmest quarter	
19	Precipitation of coldest quarter	
20	Maximum temperature of January	
21	Maximum Temperature of February	
22	Maximum Temperature of March	
23	Maximum Temperature of April	
24	Maximum Temperature of May	
25	Maximum Temperature of June	

	Predictor variables	Unit
26	Maximum Temperature of July	
27	Maximum Temperature of August	
28	Maximum Temperature of September	
29	Maximum Temperature of October	
30	Maximum Temperature of November	
31	Maximum Temperature of December	
32	Mean Temperature of January	
33	Mean Temperature of February	
34	Mean Temperature of March	
35	Mean Temperature of April	
36	Mean Temperature of May	
37	Mean Temperature of June	
38	Mean Temperature of July	
39	Mean Temperature of August	
40	Mean Temperature of September	
41	Mean Temperature of October	
42	Mean Temperature of November	
43	Mean Temperature of December	
44	Minimum Temperature of January	
45	Minimum Temperature of February	
46	Minimum Temperature of March	
47	Minimum Temperature of April	
48	Minimum Temperature of May	
49	Minimum Temperature of June	
50	Minimum Temperature of July	
51	Minimum Temperature of August	
52	Minimum Temperature of September	

	Predictor variables	Unit
53	Minimum Temperature of October	
54	Minimum Temperature of November	
55	Minimum Temperature of December	
56	Precipitation of January	mm
57	Precipitation of February	
58	Precipitation of March	
59	Precipitation of April	
60	Precipitation of May	
61	Precipitation of June	
62	Precipitation of July	
63	Precipitation of August	
64	Precipitation of September	
65	Precipitation of October	
66	Precipitation of November	
67	Precipitation of December	
68	Elevation	m.a.s.l