Regional level risk factors associated with the occurrence of African swine fever in West and East Africa

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Abstract

Background: African swine fever (ASF) causes severe socio-economic impacts due to high mortality and trade restrictions. Many risk factors of ASF have been identified at farm level. However, understanding the risk factors, especially wild suid hosts, determining ASF transmission at regional level remains limited.

Methods: Based on ASF outbreak data in domestic pigs during 2006–2014, we here tested, separately for West and East Africa, which risk factors were linked to ASF presence at a regional level, using generalized linear mixed models.

Results: Our results show that ASF infections in the preceding year was an important predictor for ASF presence in both West and East Africa. Both pig density and human density were positively associated with ASF presence in West Africa. In East Africa, ASF outbreaks in domestic pigs were also correlated with higher percentages of areas occupied by giant forest hogs and by high-tick-risk areas.

Conclusions: Our results suggest that regional ASF risk in East Africa and in West Africa were associated with different sets of risk factors. Regional ASF risk in West Africa mainly followed the domestic cycle, whereas the sylvatic cycle may influence regional ASF risk in East Africa. With these findings, we contribute to the better understanding of the risk factors of ASF occurrence at regional scales that may aid the implementation of effective control measures.

Keywords: Domestic cycle, Sylvatic cycle, Wild suid, Giant forest hog, Habitat fragmentation, Ornithodoros moubata
pathways in Africa and concluded that the domestic cycle may occur throughout sub-Saharan Africa, whereas the sylvatic cycle might be found mainly in East, Central and Southern Africa, where warthogs are present [8].

A few studies have been conducted to investigate the factors linked with ASF risk [10]. For the domestic cycle, the density or the herd size of domestic pigs has been considered to be positively associated with ASF outbreaks at farm level [9, 14]. Farms with traditional free-ranging husbandry systems typically experience higher ASF risk, presumably due to low biosecurity [15]. Previous occurrence of the disease on a farm and infected neighbouring farms has also been found to promote the chance of ASF infection [16]. In addition to these risk factors, ASF spread in the domestic cycle has been linked to trade-related factors [16, 17], such as the density of the road network and water bodies [14]. In fact, the movements of infected domestic pigs might be the most important factor for ASF spread in some regions, especially in West Africa where the domestic cycle is considered the only transmission pathway [7, 10, 18]. For the sylvatic cycle, the common warthog has been considered the most important vertebrate host for the circulation of ASF virus [13, 19]. Interspecific transmission between warthogs and domestic pigs may occur indirectly through *Ornithodoros* ticks, especially when pigs that share grazing areas with warthogs are bitten by infected ticks, or during human interference when wart-hog carcasses with infected ticks are transported [10]. Bushpigs (*Potamochoerus larvatus*) can also spread ASF to domestic pigs via ticks, but they are generally considered less important than warthogs due to their lower population densities, nocturnal habits, and limited contact with pigs and soft ticks [13, 20]. Finally, the red river hog (*Potamochoerus porcus*) and the giant forest hog (*Hylochoerus meinertzhageni*) can also be infected [13]. However, neither species seems to play an important role in ASF transmission due to their limited/restricted distributions [13].

To date, risk factors have predominantly been identified at farm level, whereas the influence of risk factors such as the role of wild suids and tick distribution on the dynamics of ASF transmission at larger spatial scales is not well understood [8, 10]. Understanding regional risk factors of infectious diseases is necessary for revealing the underlying epidemiological processes that might lead to important implications for control at regional scales [1, 21, 22]. Therefore, the present study aims to identify the risk factors that are associated with ASF occurrence at a regional scale in Africa. Due to the potentially different ASF transmission pathways, we compare the risk factors between West Africa and East Africa. We expect that the presence of wild suids and tick distribution is positively associated with the probability of ASF occurrence in East Africa, whereas domestic pig density and indicators of trade activities have a positive effect in West Africa.

**Methods**

**African swine fever data**

Data on ASF presence/absence in domestic pigs for some countries in the sub-Saharan Africa from 2005 to 2014 is available in the World Animal Health Information (http://www.oie.int/wahis_2/public/wahid.php/WahidHome/Home) from the World Organization for Animal Health (OIE) [23], which provides data on ASF outbreaks at a temporal resolution of 6 months. Some African countries reported ASF outbreaks only at country level, while other countries specified ASF outbreaks at a smaller administrative level. The smallest administrative level of reporting was used as the level of analyses in this study, whilst those countries reporting ASF outbreaks only at country level were excluded from the study.

Only the countries with “ASF history” (at least one outbreak was reported during the study period) were included in the analyses, as this excluded those countries which had possibly ASF outbreaks but never reported them, so that we avoided some false absence data. Thus, we assumed that no report from a country/administrative unit that had previously reported ASF is indicative of the absence of disease for that year. In addition, to determine the effect of previous infection status, we only involved the administrative areas from the countries that reporting ASF outbreaks in more than two consecutive years. Areas without domestic pigs were excluded. The data set yielded from OIE included eleven countries (Angola, Benin, Burkina Faso, Cameroon, Ghana, Mozambique, Malawi, Nigeria, Rwanda, Togo, and Zambia). As we compared East Africa and West Africa, we then, according to the definition of Statistics Division of the United Nations (http://millenniumindicators.un.org/unsd/methods/m49/m49.htm), excluded Angola and divided the remaining ten countries into East Africa and West Africa. The final dataset (Additional file 1: Table S1, Figure S1) for the analyses of West Africa consisted of 1287 cases of ASF presence/absence data covering six countries and 177 administration areas, and the final data-set for East Africa included 394 cases of presence/absence data covering four countries and 51 administration areas.

**Data of the predictors**

As the infection status of the previous year (PreInf) has been linked to ASF risk in earlier studies, we tested its effect to determine the dependency of ASF status between years. We also tested for the effect of the domestic pig density (Pig) on the risk of ASF occurrence. As indicators of trade activities, road density (Road) and
human population density (Human) were calculated for each administrative area (Table 1).

Since ASF risk might be influenced by the occurrence of some wild suid species, we calculated the percentage in each administrative area that is occupied by the common warthog, the bushpig, the red river hog, and the giant forest hog and tested whether or not the wild suid species occurrences were correlated with ASF occurrence. The distributions of these species were obtained from the African Mammal Databank (AMD), a GIS-based databank of the distribution of medium to large mammals in Africa [24, 25]. For each species, AMD includes two polygon coverage files respectively describing the distribution of suitable habitat and the distribution of species occurrence at a 1 × 1 km resolution [24, 25]. The intersection of these two distribution maps was calculated as the ‘actual distribution’ for each species (Boitani et al. [25]). The percentage of protected area within an administrative area (PDA) was also included in the analysis since it was expected to hold a higher density of wild suids, increasing ASF risk. Habitat structure can influence ASF transmission by affecting host distribution and movements [13, 26]. Therefore, some habitat related predictors were incorporated in the analyses. For each administrative area, we first calculated the percentage of suitable habitat (Habitat) based on a detailed (300 m) global land cover dataset (GlobCover by European Space Agency). Twelve out of 23 land-use types were combined to calculate the areas that can sustain grazers (see Additional file 1: Table S2), i.e. grassland and open woodland that are used by livestock and several of the most important wild hosts. Based on the map of grazing area, we calculated the Mean Nearest Neighbour (MNN) and Mean Proximity Index (MPI) to test the effect of fragmentation and isolation on the risk of ASF occurrence. MNN, as a measure of patch isolation, represents the average shortest distance of patches that can sustain grazers in an administrative area to the closest similar patch. For each patch, the size and mean distance to all neighbouring patches of the same type was calculated to provide the index of MPI, which measures the degree of isolation and fragmentation [27].

In addition, climate can affect ASF transmission dynamics by influencing the biology of the host, climatic variables. The analyses included the mean temperature and precipitation during the current and preceding year (Table 1).

| Description of data                                      | Abbreviation | Units       | Mean ± SD                      |
|---------------------------------------------------------|--------------|-------------|--------------------------------|
| Biotic variables                                        |              |             | West Africa                East Africa   |
| Pig density                                             | Pig          | n/km²       | 561 ± 732                  885 ± 1679 |
| Common warthog                                          | WarthogC     | –           | 0.47 ± 0.46                 0.86 ± 0.15 |
| Bushpig                                                 | BushpigC     | –           | na²                         0.91 ± 0.12 |
| Red river hog                                           | RiverhogC    | –           | 0.45 ± 0.47                 na²          |
| Giant forest hog                                        | ForesthogC   | –           | 0.06 ± 0.21                 0.31 ± 0.41 |
| Human population density                                | Human        | n/km²       | 178 ± 286                   273 ± 310  |
| Road density                                            | Road         | km/km²      | 15.7 ± 14.5                 64.6 ± 65.8 |
| Mean tick risk                                          | TickRiskMean | –           | na²                         0.26 ± 0.12 |
| Area with high-tick-risk                                | TickRisk2    | –           | na³                         0.44 ± 0.35 |
| Area with high-tick-risk                                | TickRisk4    | –           | na³                         0.17 ± 0.20 |
| Area with high-tick-risk                                | TickRisk6    | –           | na³                         0.03 ± 0.10 |
| Habitat related variables                               | Habitat      | –           | 0.87 ± 0.21                 0.73 ± 0.20 |
| Measure of the degree of isolation and fragmentation     | MPI          | –           | 886 ± 2563                  4214 ± 7233 |
| Mean nearest neighbour                                   | MNN          | m           | 750 ± 1041                  1611 ± 1036 |
| Percentage of protected area                            | PDA          | –           | 0.18 ± 0.23                 0.17 ± 0.16 |
| Climatic variables                                      |              |             |                               |
| Annual mean temperature                                 | TemMean      | °C          | 28.2 ± 1.08                 20.9 ± 2.17 |
| Mean temperature in preceding year                      | PreTemMean   | °C          | 279 ± 1.09                  21.1 ± 2.13 |
| Annual mean precipitation                               | RainMean     | mm          | 101 ± 31.1                  101 ± 24.3  |
| Mean precipitation in preceding year                    | PreRainMean  | mm          | 97.4 ± 32.0                 94.0 ± 22.0 |

*a There is no bush pig in West Africa and no red river hog in East Africa, tick risk variables were not included in the analyses of West Africa
pathogen, and vector [28, 29]. Precipitation and
temperature can affect ASF transmission by influencing
the movements and habitat use of wild suid species. For
example, in the dry season and under high temperature
conditions, wild suids aggregate at small water ponds,
which might facilitate ASF transmission [30]. Therefore,
the annual mean temperature and mean precipitation
(Table 1) were calculated from the Climate
Research Unit (CRU) datasets [31], a time-series dataset
that yields month-by-month variations in climate from
1900 to 2010 with a grid cell of 0.5 × 0.5 degree. Because
of the adaptive process of hosts and ticks, the climatic
variables might show lag-effects on pathogen transmis-
sion [32, 33]. We thus also tested the effects of the
temperature and precipitation conditions in the preced-
ing year.

Map of tick risk
To investigate the role of the sylvatic cycle, we also
tested the effect of the distribution of the tick vector O.
moubata on ASF spread at the regional scale. O. mou-
bata is considered to be an important tick vector for
ASF [13]. The presence data of O. moubata (more than
200 records) was accessed through the VectorMap data
portal (http://www.vectormap.org). Then we applied
species distribution modelling with a machine learning
technique, namely maximum entropy modeling (Maxent
v.3.3.3 k) [34] to generate the distribution map of O.
moubata, using 19 data layers as predictors (Additional
file 1: Table S3) containing bioclimatic variables at 30
arc-seconds spatial resolution, acquired from the World-
Clim dataset (http://worldclim.org). The model with 10
subsampling runs using a random test percentage of
20% was constructed with default settings in Maxent
[35]. We included all variables as a full model and did
not remove highly correlated predictors, because we
focused on the explanatory power of the model and
multicollinearity is known to have little effect on model
fit [36]. The average AUC score (the area under the
Receiver Operating Characteristic curve) for the full
model was 0.928 ± 0.010. Based on this model, we gener-
ated a map representing the probabilities of tick pres-
ence (Additional file 2: Figure S1).

With the tick distribution map, we averaged the prob-
abilities of tick presence for each administrative area
(TickRiskMean). We also arbitrarily set three probability
values (0.2, 0.4 and 0.6) as the thresholds of high-tick-
risk, and consequently calculated the percentages of area
with high-tick-risk (areas with the probability of tick
presence higher than 0.2, 0.4, and 0.6, respectively) for
each administrative area, and got another three mea-
sures of tick risk (TickRisk2, TickRisk4, TickRisk6). As
O. moubata was predicted to be present in very few
administrative areas in West Africa (Additional file 2:
Figure S1), the tick risk variables were only included
in the analyses of East Africa. In addition, to test the
effect of tick-suid interactions, we also included the
interaction terms between tick risk variables and wild
suid variables.

The data for all predictor variables were acquired or
generated from existing databases (Additional file 1:
Table S4). All data pre-processing was carried out in
ArcGIS v10.0.

Statistical analyses
Generalized linear mixed models (GLMM) with a binary
response (logit link) were used to examine the effects of
predictors on the probability of ASF occurrence. Coun-
try was included in the models as a random factor to
control for possible differences between countries,
thereby correcting for the effect of differences in veteri-
ary service efficiency and used control measures. Only
the ASF presence/absence data from 2006 to 2014 were
used as the dependent variable, because the earliest year
in the dataset was 2005, which was used to calculate the
previous infection status (PreInf) for 2006. Before per-
forming the GLMMs, we log-transformed Pig, Human,
Road, MPI and MNN, making these variables closer to
normal distribution. All continuous variables were
rescaled to have a mean of zero and a standard deviation
of one.

Using GLMMs, we first performed univariate analyses
to identify the potential risk factors. The area of the unit
(Area) was retained in the model as an obligate variable
to correct for the effect of area size. Variables with a P-
value of less than 0.15 were identified as potential risk
factors, which were used to construct multiple regres-
sion models. We then assessed multi-collinearity by
examining the variance inflation factor (VIF) of the can-
didate variables. For highly correlated independent vari-
ables, only the one with the smallest P-value in the
univariate analyses was maintained in fitting the multiple
regression models to avoid multi-collinearity. To con-
struct the final multiple model, we used both backward
and forward selection, where the likelihood ratio test
was applied to test for difference in the fit of the nested
models. For both West and East Africa, backward and
forward selection generated same models. We then in-
cluded interaction terms after including all main factors.
Main terms were maintained in the model if they were
included in a significant interaction term. We tested for
the spatial autocorrelation of the residuals (of the final
multiple model) using Moran’s I index and found little
evidence of spatial autocorrelation (Additional file 2:
Table S1). The AUC scores for the final models were
also reported to assess the goodness-of-fit. The whole
statistical processes were conducted in R 2.15.1 with
lme4 [37].
**Results**

**Descriptive epidemiology**

Over the entire study period, 25.0% of the administrative areas in West Africa reported ASF occurrence, whereas in East Africa this was 21.0% (Table 2).

**Univariate analyses of risk factors**

Twenty potential risk factors were individually tested using univariate regression analyses (Table 3). Previous infection status (PreInf) was positively associated with ASF occurrence in domestic pigs both in West and East Africa. Besides, five biotic factors (Pig, Human, Road, WarthogC, and RiverhogC), four climatic factors and one related to grazing area (Habitat) were significantly correlated with ASF occurrence in West Africa. In East Africa, besides PreInf, only three biotic variables (ForesthogC, WarthogC and TickRisk4) and two climatic variables (TemMean and PreTemMean) were significantly associated with ASF occurrence in domestic pigs.

**Multiple regression models**

After checking for collinearity, nine variables (PreInf, Pig, WarthogC, RiverhogC, Human, Road, Habitat, PDA, PreTemMean and RainMean) were retained to construct the final multiple regression models for West Africa, and five (PreInf, WarthogC, ForesthogC, TickRisk4, and PDA) were retained for East Africa. For West Africa, the results of stepwise model selection (Table 4) showed that ASF occurrence in domestic pigs was positively associated with previous infection status (PreInf, OR = 4.63, 95% CI: 3.92–5.46, \(P < 0.001\)), pig density (Pig, OR = 1.32, 95% CI: 1.19–1.46, \(P = 0.007\)) and human population density (Human, OR = 1.36, 95% CI: 1.23–1.51, \(P = 0.002\)), though many variables were significantly correlated with ASF presence in the univariate analysis. The area under the ROC curve (AUC) for the final multiple model for West Africa was 0.785. For East Africa, previous infection (PreInf, OR = 2.40, 95% CI: 1.84–3.14, \(P = 0.001\)), percentage of the area occupied by forest hog (ForesthogC, OR = 2.14, 95% CI: 1.63–2.81, \(P = 0.005\)), and the percentage of area with high-tick-risk (TickRisk4, OR = 6.98, 95% CI: 1.22–39.85, \(P = 0.029\)) had positive relationships with ASF occurrence in domestic pigs. No interaction terms was significantly correlated with ASF presence in East Africa. The AUC for the final multiple model in East Africa was 0.780.

**Discussion**

Many previous studies have been conducted to investigate risk factors for ASF transmission at farm level [9, 10, 14, 16]. However, understanding of the factors affecting regional disease risk remains limited. Here, we tested which factors were correlated with the probability of ASF presence in domestic pigs at regional scale in Africa. Our study identified different sets of risk factors in West Africa and East Africa. Previous infection status was positively correlated with ASF occurrence in domestic pigs in both West and East Africa, suggesting that for both West and East Africa greater effort should be made to control ASF in those areas that have experienced ASF outbreaks in the past. Pig density and human density were also positively associated with regional ASF occurrence in West Africa, where ASF transmission follows the domestic cycle. In East Africa, the percentage of the area where giant forest hog occurred, and the high-tick-risk area, were positively linked to ASF occurrence in domestic pigs, suggesting that the sylvatic cycle is of epidemiologic importance here.

**West Africa**

In line with previous studies [10, 16], the effect of the previous infection status (PreInf) on ASF presence in domestic pigs in West Africa indicates that ASF occurs

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**Table 2** The number of infected areas, regional prevalence of ASF occurrence in West and East Africa

| Year | West Africa | East Africa |
|------|-------------|-------------|
|      | No. of area | No. of area | |
|      | Infected areas | Infected areas | Infected areas |
|      | Infection prevalence (%) | Infection prevalence (%) | Infection prevalence (%) |
| 2005 | 13 | 7 | 98 | 25 | 0.255 |
| 2006 | 51 | 12 | 98 | 16 | 0.163 |
| 2007 | 51 | 9 | 177 | 34 | 0.192 |
| 2008 | 51 | 11 | 177 | 35 | 0.198 |
| 2009 | 51 | 9 | 177 | 40 | 0.226 |
| 2010 | 51 | 18 | 177 | 52 | 0.294 |
| 2011 | 44 | 12 | 116 | 17 | 0.147 |
| 2012 | 44 | 9 | 151 | 31 | 0.205 |
| 2013 | 44 | 18 | 151 | 35 | 0.232 |
| 2014 | 44 | 6 | 151 | 25 | 0.166 |
| Total | 444 | 111 | 904 | 202 | 0.210 |
repeatedly in the same area. In West Africa, where the domestic cycle dominates, the endemcity of ASF might be caused by the long persistence of the ASF virus which, shed by infected pigs or asymptomatic carriers, can remain in the environment for a long time [38]. In addition, the significant relationship of previous infection status might be caused by those factors that were not considered in the analyses but associated with the previous ASF occurrence, such as within-country variation in the quality of veterinary service or used control measures.

We showed that both pig density and human density were positively correlated with regional ASF occurrence in West Africa, which was also in line with previous studies [9], suggesting that the domestic cycle is indeed dominant in West Africa. A higher pig density implies a higher probability for susceptible pigs to contact infected pigs or pork products [39], contributing to the spread and persistence of ASF virus [9, 40]. Thus, the probability of ASF presence is higher with increasing pig density. Higher human population density, which was used as the surrogate of trade activity [41, 42], may also facilitate ASF spread. In fact, pig movement and trade activity have been considered as important factors for ASF spread, especially in West Africa where the domestic cycle is dominated [10, 11, 17]. As expected, no wild suids showed a significant relationship with ASF occurrence, suggesting that the sylvatic cycle may not play an important role in ASF transmission at regional scales in West Africa.

### East Africa

Our results from East Africa also identified previous infection status (PreInf) as a predictor for ASF occurrence in domestic pigs at regional scales. The endemcity of ASF in East Africa might be stimulated by the sylvatic cycle where infected wild suids and ticks can maintain the virus, transmit the virus to domestic pigs, and contribute to ASF persistence. Asymptomatic carriers of wild suids may also facilitate the persistence of ASF in East Africa [10]. We also found a positive relationship between ASF risk and the area with high risk of ticks, indicating that the sylvatic cycle may play an important role in ASF spread in East Africa. Previous studies have documented the importance of warthogs in the sylvatic cycle in East Africa. However, we did not find a significant effect of warthog distribution in East Africa. This might be caused by the limitation of our warthog data.

### Table 3

| Variables | West Africa (n = 727) | | | East Africa (n = 217) | | | |
|-----------|-----------------------|------------------|------------------|-----------------------|------------------|------------------|
|           | b | Z-value | P-value | b | Z-value | P-value |
| PreInf    | 1.64 | 10.03 | < 0.001*** | 1.02 | 3.88 | < 0.001*** |
| Pig       | 0.404 | 3.97 | < 0.001*** | -0.026 | -0.15 | 0.880 |
| WarthogC  | -0.27 | -3.62 | 0.003** | -0.24 | -2.03 | 0.043* |
| BushpigC  | na* | na* | na* | 0.026 | 0.189 | 0.850 |
| RiverhogC | 0.363 | 3.77 | 0.001* | na* | na* | na* |
| ForesthogC | 0.128 | 1.453 | 0.146 | 0.81 | 3.04 | 0.002** |
| TickRiskMean | na* | na* | na* | 2.44 | 1.47 | 0.14 |
| TickRisk2 | na* | na* | na* | 0.32 | 0.54 | 0.59 |
| TickRisk4 | na* | na* | na* | 1.99 | 2.38 | 0.017* |
| TickRisk6 | na* | na* | na* | 2.33 | 1.61 | 0.11 |
| Human     | 0.384 | 4.71 | < 0.001*** | 0.42 | 1.37 | 0.170 |
| Road      | 0.530 | 4.34 | < 0.001*** | 0.522 | 1.12 | 0.264 |
| Habitat   | -0.304 | -4.00 | < 0.001*** | 0.040 | 0.293 | 0.769 |
| MPI       | 0.044 | 0.500 | 0.616 | 0.311 | 1.11 | 0.267 |
| MNN       | 0.116 | 1.33 | 0.184 | 0.240 | 1.32 | 0.186 |
| PDA       | -0.089 | -1.08 | 0.280 | 0.308 | 1.93 | 0.053 |
| TermMean  | -0.21 | -2.01 | 0.043* | 0.213 | 0.608 | 0.543 |
| PreTermMean | -0.29 | -2.75 | 0.006** | 0.268 | 0.737 | 0.461 |
| RainMean  | 0.34 | 3.61 | 0.001*** | 0.052 | 0.346 | 0.729 |
| PreRainMean | 0.19 | 2.12 | 0.033* | 0.112 | 0.720 | 0.472 |

*There is no bush pig in West Africa and no red river hog in East Africa. Tick risk was not included in the analyses in West Africa

*P < 0.05; **P < 0.01; ***P < 0.001

### Table 4

| Variables | West Africa (n = 727) | | | East Africa (n = 217) | | | |
|-----------|-----------------------|------------------|------------------|-----------------------|------------------|------------------|
|           | b ± SE | OR (95% CI) | P-value | b ± SE | OR (95% CI) | P-value |
| PreInf    | 1.53 ± 0.16 | 4.63 (3.92–5.46) | < 0.001*** | 0.88 ± 0.27 | 2.40 (1.84–3.14) | 0.001** |
| Pig       | 0.28 ± 0.10 | 1.32 (1.19–1.46) | 0.007** | 0.76 ± 0.27 | 2.14 (1.63–2.81) | 0.005** |
| Human     | 0.31 ± 0.10 | 1.36 (1.23–1.51) | 0.002** | 1.94 ± 0.89 | 6.98 (1.22–39.85) | 0.029* |

*P < 0.05; **P < 0.01; ***P < 0.001
Due to the lack of the data of warthog densities, we could only use the percentage of area covered by warthog distribution (WarthogC) as a surrogate to test for the effect of warthog on ASF occurrence. However, in our analyses all administrative areas in East Africa had an occurrence of warthog (WarthogC > 0). The small variation of WarthogC (86 ± 15% SD, Table 1) precluded it to be a good variable to test for the effect of warthogs.

It has been considered that the giant forest hog is unlikely to play an important role in ASF transmission as its distribution is restricted to areas of dense forest where domestic pig production is not common [13]. However, here we show a significant positive relationship between ASF presence and the occurrence of giant forest hog (ForesthogC), indicating that giant forest hog might promote ASF risk at a regional scale in East Africa. This suggests the presence of the sylvatic cycle in East Africa. At a regional scale, giant forest hog may promote an increase in the density of tick vectors or transmit ASF to other wild suid species that share the same habitats, and thus increases regional ASF risk. Certainly, the positive effect of giant forest hog might be caused by some unidentified factors that was correlated with giant forest hog. For example, it could be that in areas where forest hog occur there are high densities of warthog that facilitate ASF transmission. In any case, more study is needed to better understand the effect of giant forest hog on ASF transmission at regional scale.

Conclusions are not easy to be drawn from large-spatial-scale, correlative studies with data from different sources, due to the complexity of the natural environment and the difficulty of controlling confounding factors [43]. Some variables, such as the quality of the veterinary services or used control measures, could not be taken into account because of lack or incompleteness of data. However, the random factor country used in the analyses, controlled, to some extent, for the variation caused by these variables at country level. In addition, the difficulties of getting harmonized and accurate data of ASF presence/absence might influence the precision of this analysis. Especially, the information from the OIE system might under-estimated the true ASF outbreaks because of several reasons, such as clandestine pig sales or ineffective reporting systems due to lack of budget or change in administration. This under-reporting issue can limit the generality of our results. Despite these limitations, our study, for the first time, tests for the effect of biotic and climatic factors on ASF presence at regional level in Africa.

Conclusions
Our study showed that the factors that play an important role in ASF transmission at farm level, like previous infection status and domestic pig density, also link to ASF disease dynamics at regional level. We also demonstrated that ASF occurrence in East and West Africa was associated with different sets of predictors. For West Africa, we found support for the importance of the domestic cycle in ASF transmission where the ASF virus mainly spreads via direct contact between domestic pigs or between pork products and pigs. In East Africa, we show that the distribution of the tick vector and the giant forest hog were correlated to the probability of ASF presence at regional level, but more efforts are still needed to better understand the sylvatic cycle and the role of wild suids in the epidemiology of ASF at this level. Our results are relevant for developing more effective control strategies for ASF spread as they highlight variation in the regional correlates of ASF outbreaks.

Additional files

Additional file 1: Additional information for data used in analyses. (DOCX 242 kb)

Additional file 2: Additional information for the results of analyses. (DOCX 154 kb)

Abbreviations
AMD: African mammal databank; ASF: African swine fever; AUC: Area under ROC curve; CI: Confidence interval; CRU: Climate Research Unit; GLMM: Generalized linear mixed model; OIE: World Organization for Animal Health; OR: Odds ratio; ROC curve: Receiver operating characteristic curve; SD: Standard deviation; VIF: Variance inflation factor

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Availability of data and materials
The sources of all the data sets supporting the results of this article are included in Additional file 1.

Authors’ contributions
ZYXH, WFdB, FvL and MN designed the study. ZYXH collected the data. ZYXH and KJH analyzed the data and wrote the first draft. All authors contributed to revising the article. All authors read and approved the final manuscript.

Competing interests
The authors declare that they have no competing interests.

Consent for publication
Not applicable.

Ethics approval and consent to participate
Not applicable.
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