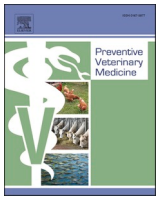
Preventive Veterinary Medicine 208 (2022) 105750



Contents lists available at ScienceDirect

Preventive Veterinary Medicine

journal homepage: www.elsevier.com/locate/prevetmed





Effects of habitat fragmentation and hunting activities on African swine fever dynamics among wild boar populations

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ARTICLE INFO

Keywords:
African swine fever
Simulation modeling
Individual-based model
Wild boar ecology
Disease ecology

ABSTRACT

African Swine Fever (ASF) has been slowly but steadily increasing its endemic range throughout Europe, posing an imminent risk to the pig industry. ASF transmission among wild boar occurs mainly through wild boar population movements, hence wild boar presence and density are important risk factors for introducing, maintaining, and spreading the disease. The understanding of wild boar population dynamics and their role in ASF transmission and persistence remains limited. It is crucial to gain knowledge in this area to improve wildlife management while minimizing the risks for ASF introduction and spread. We adapted an individual-based spatio-temporal stochastic model developed by Halasa et al. (2019) and tailored it to two regions in France. The model assessed yearly hunting activity, the carcass persistence seasonality, and the specific landscape characteristics of the Franco-Belgian border region and the Pyrénées-Atlantiques department. Following the establishment of local population dynamics through preliminary runs of the model, the model was run 100 iterations over 8 years in the two study areas where ASF was randomly seeded after the 2nd year of simulation. For each scenario, the model was initiated with 500 wild boar groups randomly spread across the study areas. Hunting activities were included and excluded to assess the impact on population growth and ASF spread. Results showed an ever-growing wild boar population for all scenarios, which was balanced when hunting activities were included. When introducing ASF, the wild boar populations were dramatically impacted in both areas with a decrease of 63 % of the population at the Franco-Belgian border and 86 % in the *Pyrénées-Atlantiques* department. Habitat fragmentation and landscape connectivity were highlighted as important factors shaping ASF propagation. The Franco-Belgian border, which had the most fragmented habitat with unsuitable areas for wild boars, was shown to limit wild boar movements, reducing the probability, and spread of ASF across the landscape. The lack of connectivity was reflected in a less effective transmission and lower number of infected groups (406 versus 467). In contrast, the epidemic duration was lengthened in the fragmented habitat compared to the homogenous area (2.6 years vs 1.6 years). This study provided information on defining and implementing control measures in case of an ASF incursion, since delimitation of the area via fences artificially induces landscape fragmentation, which is important for controlling ASF outbreaks.

1. Introduction

African Swine Fever (ASF) is a devastating hemorrhagic infectious disease caused by the African swine fever virus (ASFV). It affects wild and domestic *Suidae* with lethality rates as high as 100 %. No effective vaccine nor specific treatment exists to tackle this disease (Galindo and Alonso, 2017; Rock, 2017). ASF is classified as a Transboundary Animal Disease (TAD), due to its potential for spread, its capability for causing

Abbreviation: ASF, African swine fever; TAD, Transboundary animal disease; ASFV, African swine fever virus; FBB, Franco-Belgian border; DPA, Department of *Pyrénées-Atlantiques*.

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https://doi.org/10.1016/j.prevetmed.2022.105750
Received 8 April 2022; Received in revised form 10 July 2022; Accepted 15 August 2022
Available online 18 August 2022
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major economic losses, its impact in food security, and its ability to cause societal harm (Torres-Velez, 2019). Following the introduction of ASFV into the European continent in 2007, ASF has been slowly but steadily increasing its endemic range (Schulz et al., 2019). In Europe, ASF circulation is facilitated by pig holdings with low biosecurity measures (i.e. backyard farms), anthropogenic factors (i.e. contaminated materials, improperly disposed waste), and wild boar (*Sus scrofa*) population movements (Chenais et al., 2019; Guinat et al., 2016). Although the precise transmission mechanism between wild and domestic pigs remains unknown, domestic pig outbreaks in certain areas have been closely related to those occurring in wild boars (African Swine Fever in Europe. Updated Outbreak Asessment, 2022; Chenais et al., 2019). Hence, wild boar population presence is considered to be an important risk factor for introducing, maintaining, and circulating ASFV (Bosch et al., 2017) especially in areas with high wild boar densities (Cwynar et al., 2019). It is thus important to understand ASF dynamics in wildlife to deliver effective prevention measures in high-risk areas since wild boars' abundance and range has been steadily increasing throughout Europe (Keuling et al., 2018; Massei et al., 2014). France is considered free from ASF; however, three neighboring countries have registered outbreaks in wild boars: Belgium in September 2018 (Cwynar et al., 2019), Germany in September 2020 (Sauter-Louis et al., 2021), and Italy in early 2022 ("Animal Disease Information System (ADIS)", 2022). Therefore, a possible introduction and an imminent threat to the third-largest European swine producer cannot be ignored (Development, n.d.). For these reasons, it is crucial to understand the wild boar population dynamics (Gamelon et al., 2021, 2012) and their role in the transmission and persistence of ASFV.

Wild boar population dynamics have been previously modeled in an effort to provide useful insights for decision makers when designing effective surveillance and control strategies (Halasa et al., 2019; Kramer-Schadt et al., 2009; Lange and Thulke, 2017). Although anthropogenic factors, such as hunting activities, have an impact on population growth and dispersal (Acevedo et al., 2006; Consortium et al., 2018; Gamelon et al., 2021) they are rarely considered in epidemiological models designed for ASF. In France, hunting activities coincide with the winter season, where environmental conditions favor the preservation of carcasses and, if infected ASFV can remain viable. Thus, the probability of encountering a well-preserved infected carcass increases as hunting activities could provoke group dispersal (Scillitani et al., 2010). The objective of this study was to predict the disease dynamics in wild boars, after a hypothetical introduction in different areas of France using a spatio-temporal and agent-based model, developed by Halasa et al. (2019), and adapted to specific data of the region including the effects of hunting activities and carcass persistence in the environment.

2. Materials and methods

The study aims to simulate the spread of ASF in the wild boar population in case of introduction in two distinct geographical regions of France: in the East, at the Franco-Belgian border, and in the Southwest in the *Pyrénées-Atlantiques* department, at the Spanish border. We used data specific to those regions to assess the impact of hunting as well as the seasonal persistence of carcasses in the field.

2.1. Landscape

The area close to the Belgian border, further denoted as Franco-Belgian Border (FBB), includes the French surveillance zone for ASF control delimited by the Minister of Agriculture of France during the ASF outbreak in Belgium. To this area, we included the natural regional park of Ardennes and the natural regional park Vosges du Nord, assumed as highly suitable habitat areas for wild boars because of the forest resources (Podgorski et al., 2019). The total surface of the FBB area was 12 447 km^2. The limits of the FBB area were delimited by the country's administrative borders (Belgium, Luxemburg, and Germany), and by national highways (A-304, A-34, and N-51 at the West, the A-4 at the South, and the N-61 at the East) extracted from BDTopo® provided by the National Institute of Geographic Information and Forestry of France (IGN) (BD TOPO® | Géoservices, n.d.) (Fig. 1-A).

The second area, the department of *Pyrénées-Atlantiques* (DPA) in the South-West of France is a territory with highly dense forestry resources, hence a potentially highly populated wild boar area. The limits of the *Pyrénées-Atlantiques* department were delimited by the department administrative borders (Fig. 2-A). The total surface of this area was 8 748 km^2.

The landscape suitability for wild boar was defined by the level of forest coverage. For that purpose, data on forest coverage of each study area were extracted from the forest inventory database (BDFORET_V2®) provided by the IGN with a spatial resolution of 1:25000 (Géoportail, n.d.). The areas were rasterized into 9 km^2 cells with a spatial resolution of 1:3000. A specific number ID was given to each cell of the two grids. The FBB and DPA grids consisted of 1 383 and 972 cells, respectively. The forest coverage of each cell was intersected with the grid to define the wild boar habitat suitability (Bivand et al., 2020).

All cells were categorized based on the forest coverage and a 10 % habitat requirement threshold, as follows: 1) Suitable for wild boar (with at least 10 % forest), 2) Accessible but not suitable (between 1 % and 10 % of forest coverage), and 3) Neither accessible nor suitable (with less than 1 % of forest cover, this included cities and water bodies) (Figs. 1-B and 2-B). A passing-through probability was set depending on the habitat cells suitability, as wild boars are also present in urban areas (Ikeda et al., 2019; Podgórski et al., 2013). Habitat-category 3 cells had less permeability (i.e., 5 %) than habitat-category 2 and 1 (20 % and 75 %, respectively).

Those data were extracted into input files which contained: the identification of each cell (cell ID), the forest coverage, the coordinate centroids in longitude and latitude, and the cell ID of the 8 neighboring cells.

2.2. Model

The individual-based spatio-temporal stochastic model developed by Halasa et al. (2019) was adapted to account for hunting activity and carcass persistence seasonality without preventive and/or control measures. Based on Monte Carlo methods, the model runs on daily steps over a specific period (i.e., 8 years). The model describes the wild boar population dynamics along with the ASF transmission and spread process.

2.2.1. State variables

Two processes were simulated in the model: wild boar demographics and ASF dynamics. The mechanisms for demographics included reproduction, natural mortality, hunting mortality and related group dispersal, and natural individual mature female and male dispersal behavior.

Each wild boar was characterized by demographic, geographic (at cell level), and epidemiological information. The wild boar individual information consisted of animal ID, group ID, sex (male or female), age category (piglets: $<$ 1 year, sub-adults: between 1 and 2 years, adults: $>$ 2 years), age in days, breeding capacity (number of sows able to deliver in the group), spatial location (current pixel), day of parturition on pregnant sows, and the split status of males and females sub-adults. The epidemiological data contained the infectious status of each individual (susceptible, exposed, infected, dead, or immune), time to become infectious (latent period), time to die/be immune (infectious period), time of death of the infected individual, and carcass persistence depending on the season.

Simulation were run using R statistical software version 4.1.2 "Bird Hippe" (R Core Team, 2021). For spatial data manipulation and statistical analysis, we used the packages *raster, rgeos*, and *rgdal* (Bivand et al., 2021).Packages *tmap* (Tennekes et al., 2021) and *tmaptools* (Tennekes,

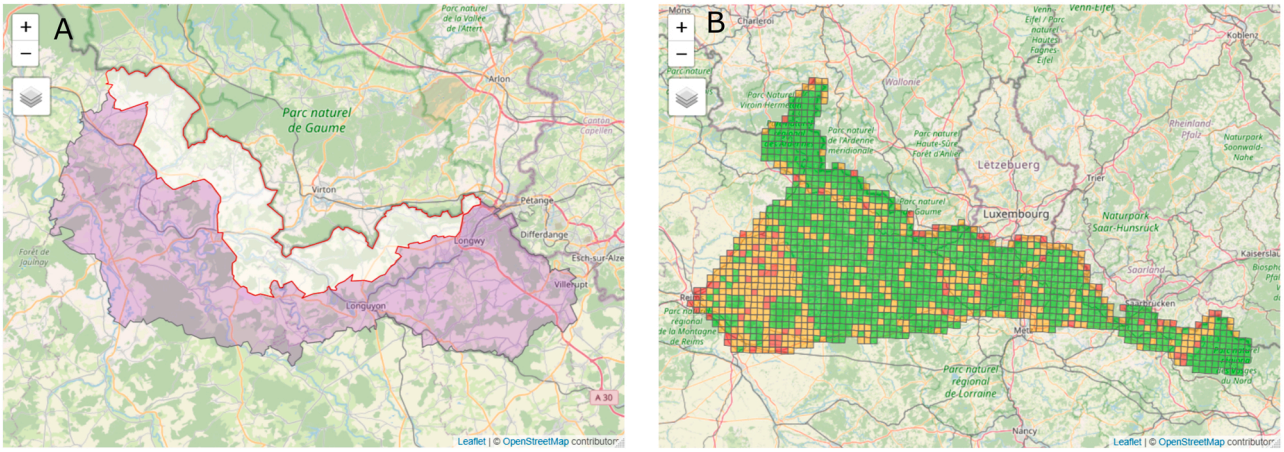


Fig. 1. Franco-Belgian delimitation zone. 1-A. Delimitation of the Franco-Belgian border zone by country borders and physical barriers corresponding to important roads and highways. Communes belonging to the restriction zone with active surveillance are included in the white zone, delimited in red; the purple area corresponds to the extended surveillance zone. 1-B. Zone considered in the model rasterized into a 9 km^2 grid; colors represented the type of habitat: green is suitable, orange is accessible but not suitable and red is not suitable but little accessible. This area was delimited by natural and artificial fences (rivers, highways or important roads). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

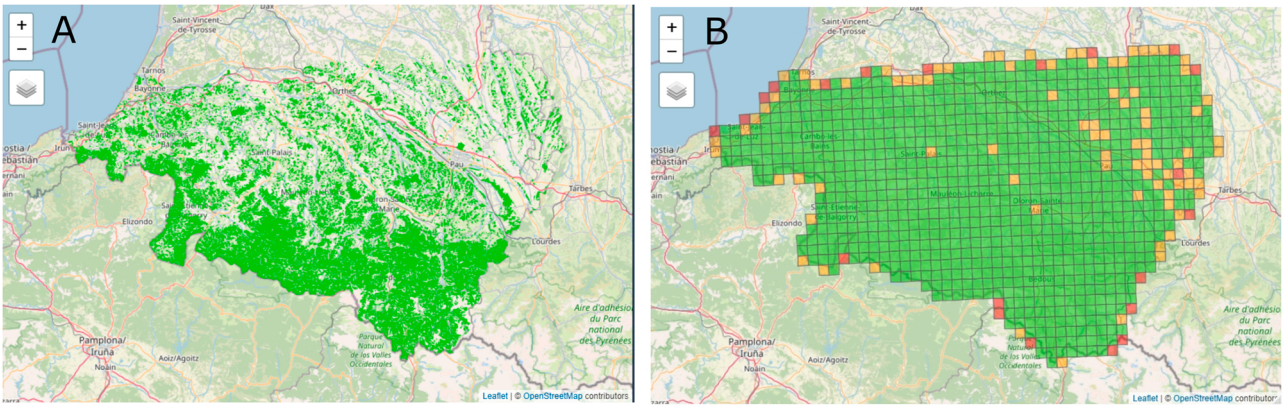


Fig. 2. *Pyrénées-Atlantiques* department zone. 2-A. *Pyrénées-Atlantiques* department and forest cover (FC) from the BDFORET_V2 database from IGN. 2-B. Zone divided into a 9 km^2 grid; colors represent each type of habitat: green is suitable (FC >10 %), orange is accessible but not suitable (10 %>FC>1 %) and red is not suitable and little accessible (FC<1 %).

2021) were used for data visualization.

2.2.2. Input data

The landscape data files for each study area described above were the only external inputs used. No changes in vegetation were assumed to occur through time. Input values and parameters used for demographic and ASF dynamics are shown in Table 1.

2.2.3. Model initialization

The model was initialized with 500 wild boar groups for each scenario; every group was randomly allocated to a suitable cell across the area. The cell assigned for a group represented the home pixel for that group and each home pixel could be occupied by only one group.

The group structure was based on the proportion of females. The number of females ranged from 1 to 8 to obtain realistic sizes for wild boar groups according to the records in France (Vassant et al., 2010).

On each time-step, each animal underwent a set of events related to demography, hunting, dispersal, or the ASF infectious process. The basics of the model were described by Keuling et al. (2013), Lange and Thulke (2017), and more recently by Halasa et al. (2019). Therefore, the processes will be briefly described, pointing out the adds-on from supplementary assumptions.

2.2.4. Submodules

This section describes the submodules in the model that correspond to the demographic and ASF dynamics.

2.2.4.1. Reproduction. Reproductive parameters were based on the original values set by Halasa et. al. (2019) where females delivered once a year randomly from January to June with a peak in March. A breeding capacity was assigned to each suitable habitat cell, defining the maximum number of mature females per group, dictating the number of females that can reproduce and deliver, which was the main driver of reproductive performance. Females for reproduction were randomly selected at the beginning of each year among adults and sub-adults. Older adult females were prioritized for breeding. The number of piglets delivered per sow ranged from 0–8 piglets.

2.2.4.2. Natural mortality. A daily mortality probability (DMP) for an individual class age A was calculated based on a yearly survival probability (YSP) as follows:

$$DMP = (1 - YSP_A)^{\left(\frac{1}{365}\right)}$$

For adult males and females, a yearly mortality of 25 % and 1 5% was considered, respectively. Similarly, for sub-adult females and sub-adult

Table 1
Parameters used in the ASF stochastic model.

Parameter	Value	Source
Wild boar groups		
Age distribution for initial groups	Adult Females: 15 % Adult males: 8 % Sub-adults: 29 % Piglets: 48 %	Halasa et al. (2019)
Age probability distribution for adult females in initial groups (year 2–10, sequentially by 1 year)	39 %, 24 %, 15 %, 9 %, 6 %, 3 %, 2 %, 1 %, 1 %	Halasa et al. (2019)
Initial number of groups	500 groups	Vassant et al. (2010)
Reproduction		
Breeding capacity (females able to deliver per cell)	PERT, minimum = 1, most likely = 4, maximum = 8	Halasa et al. (2019)
Probability distribution of number of off-spring delivered by sows (0–8 piglets, sequentially by 1)	1 %, 7 %, 16 %, 25 %, 25 %, 16 %, 7 %, 2 %, 0.1 %	Halasa et al. (2019)
Dispersal		
Dispersal for sub-adult females	If the cell breeding capacity was exceeded, and 2 sub-adults required as minimum.	Adapted from Halasa et al. (2019)
Dispersal probability of sub-adult males	50 %	Adapted from Halasa et al. (2019)
Settling probability for splitting males (in an available group)	75 %	Halasa et al. (2019)
Male walking distance	Minimum = 3 km/day Maximum = 9 km/day	Adapted from Lange, 2015
Mortality		
Minimum yearly survival probability for adults and subadults	40 %	Lange, 2015
Minimum yearly survival probability for piglets	10 %	Lange, 2015
Survival probability for adult females	85 %	Keuling et al. (2013)b
Survival probability for adult males	75 %	Keuling et al. (2013)b
Survival probability for sub-adults females	75 %	Keuling et al. (2013)b
Survival probability for sub-adult males	70 %	Halasa et al. (2019)
Survival probability for piglets (males and females)	50 %	Lange, 2015
Hunting		
Hunting Season	October to February	Toigo et al. (2008)
Probability of harvest for adults and sub-adults females and sub-adult males	40 %	Toigo et al. (2008)
Probability of harvest adults males	60 %	Adapted from Toigo et al. (2008)
Probability of group movement caused by hunting	30 %	Adapted from Toigo et al. (2008)
ASF Epidemiology		
Seed infection	Day 730	Adapted from Halasa et al. (2019)
Daily ASF transmission probability through direct contact within group (nose to nose)	0.007	Lange, 2015
Daily ASF transmission probability through carcass contact within group	0.03	Lange, 2015
Daily ASF transmission probability through carcass contact between groups (neighbor cells)	0.03	Lange, 2015
Latent period in days	PERT (minimum = 1, most likely = 5, maximum = 9)	Halasa et al. (2019)
Infectious period in days	PERT (minimum = 1, most likely = 5, maximum = 7)	Halasa et al. (2019)
Probability of death after ASF infection	95 %	Blome et al., 2012
Probability of dying in neighboring cells	80 %	Lange, 2015
Carcass persistence in days	Summer = 5, winter = 90, spring/autumn = 28	Adapted from Halasa et al. (2019)

males, yearly mortalities of 25 % and 30 % were considered. A lower mortality probability for females was considered to ensure an increasing population, these parameters were also based on field observations in France. Piglets were considered to have a mortality rate of 50% within the first year of life; piglets less than 8 weeks old that had lost their mother were assumed to die (Toigo et al., 2008).

2.2.4.3. Dispersal. Different patterns were defined according to wild boars' sex since males move more than females (Keuling et al., 2010). Female sub-adult dispersion was triggered when the breeding capacity of the cell was exceeded otherwise, they would stay in their original home pixel. Female dispersal occurred each year during week 28 (Kramer-Schadt et al., 2009). The settlement of new female groups depended on the availability of free suitable (category 1) cells in the neighborhood of their home range. It was assumed that at least 2 sub-adult females from the same group would disperse to form a new group. Females settled either in cells in which only males were present (individuals that were moving) or in empty suitable cells, whereas males could only settle if only female groups were available. The target cell was defined prior to movement and females chose the shortest pathway from their home range to the target cell, preferring to move through suitable and accessible cells when available. If there was no possibility of moving due to inaccessibility, females would find another path towards the target cell.

The male sub-adults would disperse if they were belonging to a group where male adults were already present. Splitting occurs during weeks 25–30 each year. There should be at least two sub-adult males in a group for splitting. The splitting individuals would form a new group and it would disperse to join a female group without male. The dispersal of a sub-adult males was determined by a splitting probability and using a uniform distribution (Table 1). The new sub-adult group would disperse in a semi-random walk: a random direction from a specific group home pixel was selected (i.e., North, East, South, and West) where each direction had three possible cell destinations. The direction may change based on the permeability (passing-through category) of each cell, which was the same as in female dispersal. Once a direction was assigned, one of the three possible cells in the selected direction is chosen randomly, given the accessibility of the cell. Sub-adult males could move between 1 and 2 cells every day, leading to a 14 km distance walked on average within the dispersal week although, they would stop moving after finding a suitable habitat. Sub-adult males would look for a female group to settle for reproduction objectives. Since males can walk long distances (Keuling et al., 2010), they were allowed to walk around randomly during the simulation time to find a new group to settle. The path of cells which each individual pass through was saved daily.

2.2.4.4. Hunting. In France, hunting is allowed from October to February (Toigo et al., 2008). Adult and sub-adult females, and sub-adult males have a 40 % chance of being harvested, whereas adult males have a greater chance of being harvested (i.e., 60 %). Piglets were not included in the hunting activities, as in France it is not common to target offspring. Additionally, to the hunting probability, a daily group dispersal probability triggered by hunting activities was computed

(Table 1). Groups that were targeted (i.e., with at least one harvested animal) had a movement probability of 30 %, in which the whole group looked for a suitable empty cell in the immediate neighborhood of their home pixel.

2.2.4.5. ASF dynamics. In order to seed the infection into a stable population, the virus was randomly introduced into a single individual after the second year of simulation (day 730). Transmission can occur through (i) direct contact (nose to nose) within a group and between groups in neighboring cells, or (ii) contact with an infected carcass within a group, in neighboring cells, or while dispersing. The progression of the disease in each individual follows a susceptible – exposed – infected – removed (via death or recovery) model (SEIR).

For a susceptible individual (i) that is not dispersing (nd) and that belongs to a group (g), the daily probability of infection through direct contact from infected individuals within the same group and at time step t was calculated as follows:

$$PI_{nd}^{(g)}(t) = 1 - (1 - P_{wl})^{N_{wl}^{(g)}(t)}$$

Where P_{wl} is the probability of infection through direct contact with an infected live wild boar, and $N_{wl}^{(g)}(t)$ is the number of live infected wild boars in the group (g) at the specific time step (t.) Homogeneous mixing was assumed within the group.

The probability for a susceptible individual that is not dispersing (nd) and that belongs to a group (g), of infection through contact with an infected carcass within its home pixel or neighboring pixels is calculated as follows:

$$PIC_{nd}^{(g)}(t) = 1 - (1 - P_{wc})^{N_{wc}^{(g)}(t)} * \quad (1 - P_{bc})^{N_{bc}^{(g)}(t)}$$

Where P_{wc} is the probability of infection by contact with an infected carcass in the cell, and P_{bc}.

is the probability of infection by infected carcasses that are in the neighboring cells. $N_{wc}^{(g)}(t)$ is the number of infected carcasses within a cell and at a specific step, and $N_{bc}^{(g)}(t)$ is the number of infected carcasses in the neighboring cells at a specific time.

The total probability of infection for a susceptible individual (i), that is not dispersing (nd), belonging to a group (g), during a time step (t): $PIT_{nd}^{(g)}(t)$ is calculated as follows:

$$PIT_{nd}^{(g)}(t) = 1 - \left(1 - PI_{nd}^{(g)}(t)\right) * \left(1 - PIC_{nd}^{(g)}(t)\right)$$

The probability of infection of an individual (i) that is dispersing (d) in a group (g) from a carcass within the cell path (z) during time step (t): $PIC_{(d)}^{(g)}(t)$ was calculated as follows:

$$PIC = 1 - (1 - P_c)^{\sum\left(V_Z^{(g)}(t) * N_Z^{(g)}(t)\right)}$$

Where Pc is the probability of being infected after contact with an infected carcass, N is the total number of infected carcasses in a pixel z where an individual (i) belonging to a group (g) has passed-through while dispersing during time step (t). Finally, V is the number of times a pixel z has been passed through by an individual (i) in group (g) dispersing during time step (t).

When a susceptible individual contacts an infectious unit, the susceptible individual transits to the exposed compartment during a PERT-distributed latent period of 5 (range: 1–9) days. After this period, the animal enters the infectious state for a time slot also governed by a PERT distribution latent period (Table 1): During this period, the infected individual can transmit the virus among its group. Afterwards, the animal dies or becomes immune; carcasses will remain as infectious. Persistence of infected carcasses will follow a seasonality where it will persist longer in winter season (90 days) than in summer season (5 days) (Guberti et al., 2019). In-between seasons, carcasses persist for 28 days. If an animal overcomes the disease and becomes immune, it would not be infectious nor experience re-infection (Table 1). No maternal immunity transfer from immunized sows to newborn piglets was assumed.

2.2.5. Simulation study

The model was simulated first without ASFV infection in both study areas over 5 years. For each territory, 10 iterations including and excluding hunting activities were run for comparing demographic dynamics. Subsequently, 100 iterations were run over 8 years including ASFV introduction including and excluding hunting. Here, the disease was randomly seeded into one individual at the end of the second year and the simulation continued until the end of the 8th year. If the disease faded out, the model continued simulating the demographic mechanisms to picture the wild boar populations recovering. Finally, a survival analysis was performed to study and compare the total duration of ASF epidemics in all scenarios, considering the time between the introduction of ASFV and the last effective transmission into a susceptible wild boar.

3. Results

3.1. Habitat suitability

The distribution of suitable 9km2 cells for wild boars of the two study areas is depicted in Figs. 1-B and 2-B. For the FBB area, the number of suitable cells was 902 (65.2 % of the territory) whereas for DPA was 865 cells (88.9 % of the territory). Therefore, DPA was composed of more suitable and connected habitat for wild boar populations, with 8.8 % of the land being accessible but not suitable, and only 2.2 % of them are not accessible. In the FBB area, habitat suitability was fragmented across the area except for the Western part which was poorly suitable for wild boar populations. In this area, 28.9 % of the land was accessible but not suitable, and 5.8% of the area was poorly accessible (category 3).

3.2. Without ASF – Population dynamics

For the initial 500 wild boar groups, each group occupied one suitable cell in all scenarios. When ASFV was absent, the wild boar population tended to increase with time in both study areas. A seasonal trend on the number of wild boars can be observed in the graphics due to the annual reproduction in spring, followed by a decrease due to natural yearly mortality. Population density varied between 1.5 and 3 wild boars/km2 with a median group size of 19 individuals with a 95 % confidence interval of 9–43 individuals. When annual hunting activity was included, the population continued to exhibit an overall increase though a seasonal peak still followed by a decrease was observed. The median population sizes at the time of virus introduction (day 730) were similar in FBB and DPA areas with about 21,000 individuals when excluding hunting, and 15,000 when including hunting activities (Fig. 3). The corresponding wild boar densities in the DPA landscape varied from 1.68 animals per km^2 including hunting and 2.48 animals per km^2 when excluding it. In the FBB scenario, densities varied from 1.18 to 1.73 animals per km^2 including and excluding hunting strategies, respectively.

3.3. Population and disease dynamics after ASFV introduction

3.3.1. Excluding hunting

In both areas, the introduction of the virus in one wild boar group quasi-systematically led to a transmission to neighboring groups, inducing a sudden decrease in the wild boar populations. In FBB, the median number of wild boars fell to a minimal value of 7 342 individuals on day 1 130 post-infection, corresponding to a decrease of 63% of the initial population (Fig. 4-A). In DPA, the wild boar population was even more heavily and rapidly impacted by the virus with a decrease of 85% of the population and only 2 909 individuals left at day 759 post-

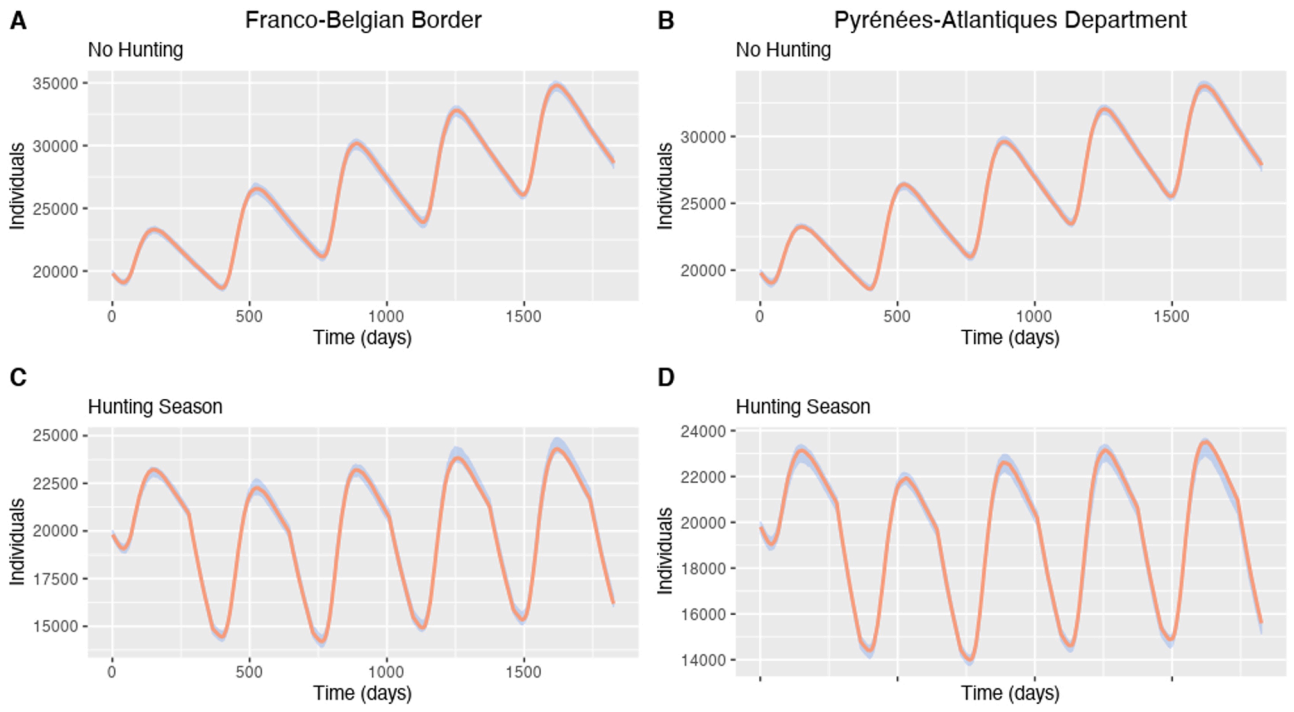


Fig. 3. Wild boar population dynamics. Wild boar population dynamics through time in both study areas in absence of ASF infection, excluding hunting (A & B) and including hunting (C & D). The orange line represents the median over 10 iteration, and blue shade the 95 % variability range.

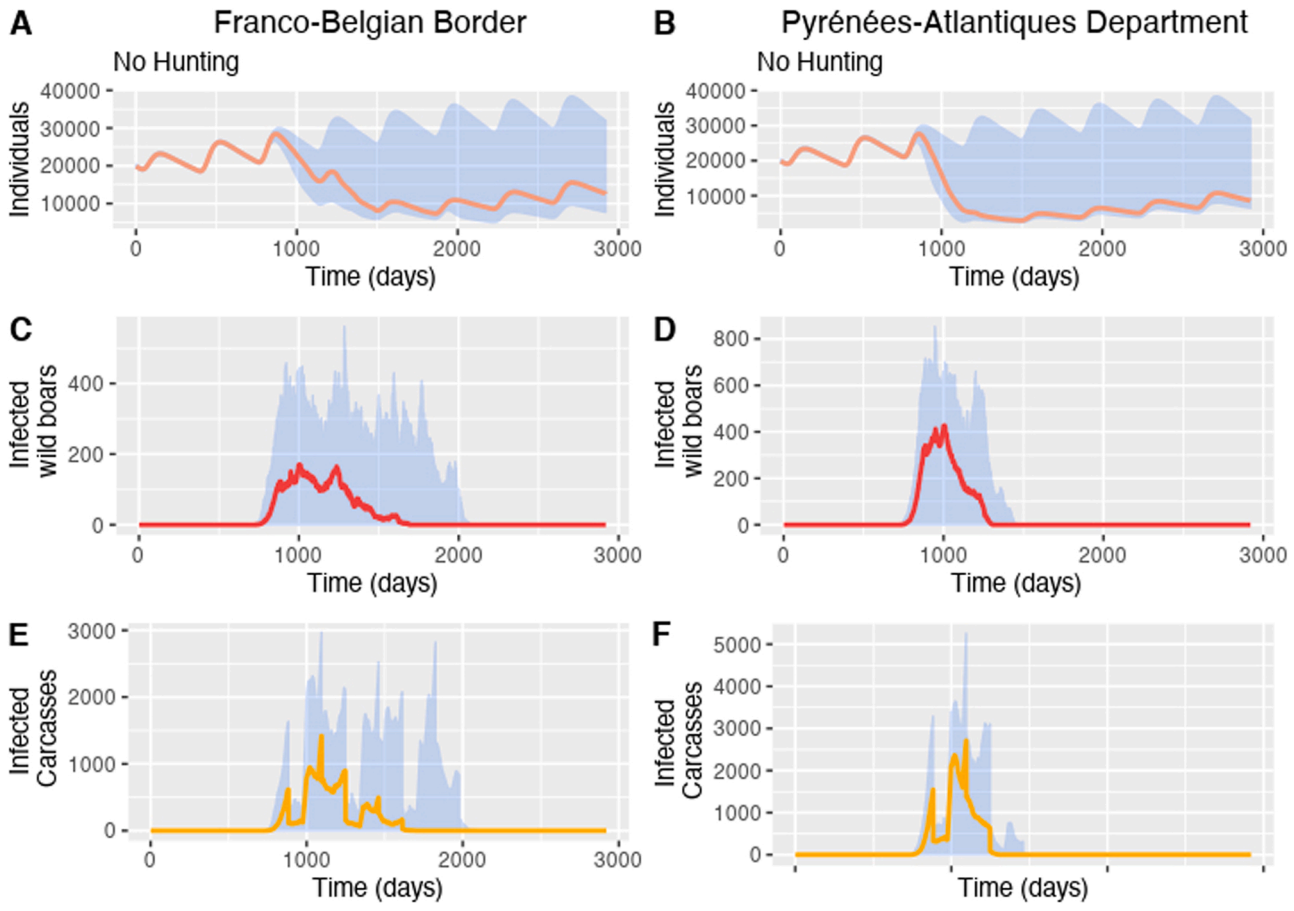


Fig. 4. ASF infection dynamics excluding hunting activities. ASF infection dynamics after random introduction of ASFV at day 730 in both study areas without hunting activities. The colored line represents the median behavior of the model and the blue shades the variabilities at 95 % (100 simulations).

introduction (Fig. 4-B).

In the fragmented FBB landscape the cumulative number of infected groups was 406 during the 8-year simulation (translated into 19,151 infected individuals). The infection dynamics showed a slow and long-lasting transmission process as the median epidemic duration was 969 days (2.6 years) and the epidemic peak at day 273 post-introduction with 170 infected individuals. In contrast, the introduction of the virus in the homogeneous DPA landscape resulted in 467 cumulative infected groups (109715 infected wild boars), 150 % higher than in the FBB area. The median epidemic duration was shorter with 589 days (1.6 years) and the epidemic peak at day 276 post-introduction with 427 infected wild boars, around 2.5 times higher than FBB (see Fig. 4-C and D).

The aggregation of infectious carcasses in the environment showed seasonal peaks reflecting the persistence in winter conditions (4-E and 4-F). For instance, on day 170 post-introduction, which represented summer season, the number of infectious carcasses in the area was 107 versus 1 297 at day 360 post-introduction, which coincided with winter season (Fig. 4-E). In the non-fragmented area (DPA), the number of infected carcasses was higher, varying between 310 in summer season and 2 492 carcasses in winter season. (Fig. 4-D).

3.3.2. *Including hunting*

The model behavior when including hunting activities was broadly similar for the two areas. Although, hunting activities had a direct impact on ASF dynamics. For instance, when including hunting, a lower transmission process to neighboring groups was observed. This was reflected by a significantly lower number of infections, but several infection waves can be seen in both areas; alongside a steady population decrease (Fig. 5C and D). The counterpart of the decrease was a significantly lengthened epidemic duration in both areas. Particularly in FBB landscape, the epidemic lasted 1 066 days (2.9 years) and consisted of 281 cumulative infected groups translated into 11,442 infected animals. A decrease of 53% of the initial population was seen with a minimum of 9 368 individuals at day 1 129 post-introduction (Fig. 5A). In comparison to the scenario without hunting, the number of infected animals in the same landscape decreased by 73%, with 45 infectious animals at the peak of infection. Although hunting activities clearly show a reduction in the transmission dynamics, the epidemic duration — the time difference in days between the introduction of ASFV and the fade-out of the disease — increased by 3.2 months (Table 2).

Conversely, the non-fragmented DPA landscape with hunting activities scenario resulted in a decrease of 83 % of the initial population with

Table 2
Median (5th - 95th percentiles) of the epidemic duration, cumulative infected animals, groups, and carcasses in the four scenarios.

Area	Hunting Season	Epidemic Duration (days)	Total Infected Animals	Total Infected Groups
FBB (Fragmented)	No	969 (745–1166)	19151 (2–22637)	406 (1 – 497)
	Yes	1066 (154–1481)	11442 (2–15826)	281 (1 – 413)
DPA (Non-fragmented)	No	589 (538–730)	19039 (3–22511)	471 (1 – 548)
	Yes	885 (790–923)	14320 (2–17035)	463 (1 – 557)

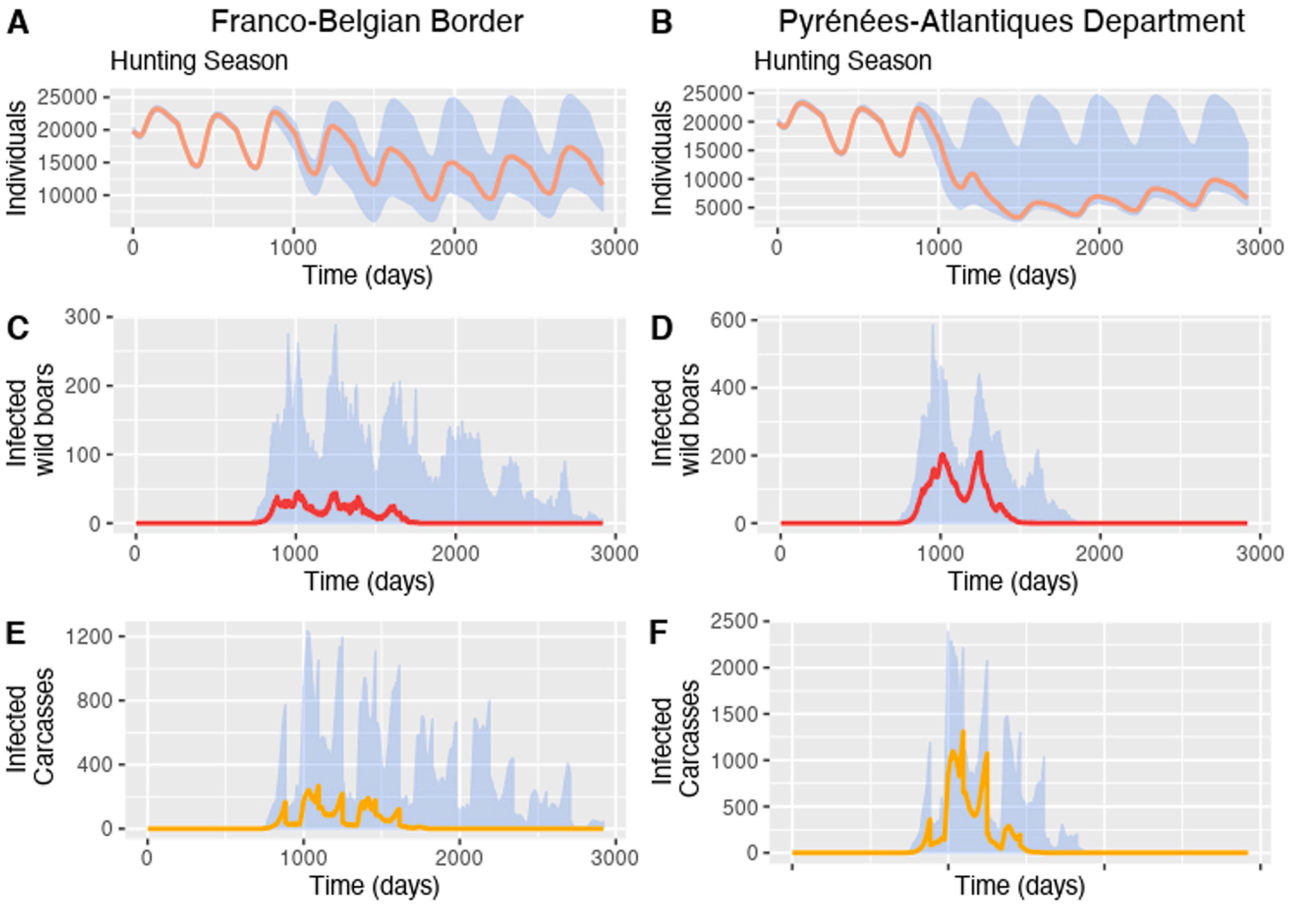


Fig. 5. ASF infection dynamics including hunting activities. ASF infection dynamics after randomly introducing the ASFV at day 730 in both areas including hunting activities during hunting season (from October to February). The colored line represents the median behavior of the model and the blue shades the variabilities at 95 % (100 simulations).

a minimum of 3 285 individuals at day 764 post-introduction (Fig. 5B). The epidemic duration lasted 885 days (2.4 years) with 463 infected groups (14,320 cumulative infected animals) and the epidemic peak happening at day 485 post-introduction with 209 infected individuals (Fig. 5D). By comparison with the DPA scenario without hunting, the number of infected animals decreased by 41 % but the epidemic duration increased by 10 months, approximately. Some simulations depicted enzootic situations where the disease lasted beyond 3.5 years in the fragmented landscape (Fig. 6). However, all simulated scenarios presented stochastic extinctions of the disease, depicted in the survival curves with differences depending on the fragmentation of the habitat (Fig. 6). Early extinctions are more common in the FBB landscape with 16–21 % of occurrence on day 120 post-introduction, whereas at the DPA area, these extinctions varied from 6% to 12% of occurrence during the same time (Fig. 6).

Excluding hunting, similarities were shown in the accumulation of infected carcasses in the environment in both areas following a seasonal persistence (Fig. 5 E and F). At FBB, one year after ASF-introduction, a total of 266 infectious carcasses were present in the environment, coinciding with the winter season. In contrast, in the summer season around 30 infectious carcasses were present in the area. These results represent a decrease of around 80% of infectious carcasses amount when comparing with the scenario excluding hunting (Fig. 5E). On the other hand, in the DPA area the maximum number of infectious carcasses was 1 307 one year after ASF introduction which coincided with winter season. During the summer season, around 100 infectious carcasses were accumulated in the area, representing 50% of the infectious carcasses accumulated without hunting (Fig. 5F). Table 2 shows the main results for comparison between the four scenarios.

4. Discussion

In this study, no changes in weather conditions nor food availability were considered during the 8-year simulation period to represent the increasing trend of wild boar populations observed in Europe (Acevedo et al., 2007; Jori et al., 2021; Massei et al., 2014; Touzot et al., 2020). In the absence of ASF, the model showed an ever-growing wild boar population which was balanced by the inclusion of hunting activities. Multiple factors can explain this wild boar expansion such as milder winters, rewilding strategies, increased food availability (i.e., intensified crop, mast production, and supplementary feeding), the species' associated environmental plasticity, or the scarcity of predators (Acevedo et al., 2006; Fernández et al., 2006; Massei et al., 2014; Oja et al., 2014; Sandom et al., 2013; Touzot et al., 2020). Although mortality caused by predators is relatively low, it can shape directly the group dynamics by removing small and young individuals (Massei et al., 2014) while hunting normally focuses on removing adult, sub-adults, and animals that have lost stripped pelage. Females are not traditionally targeted as trophies since they preserve densities and shape demographics (Keuling et al., 2013; Servanty et al., 2011).

In this study, hunting activities were shown to be a main driver for population regulation. Although the observed trend of the population was to increase, this tendency was limited in the scenarios with hunting activities, in comparison to scenarios where hunting was not accounted for. Whilst hunting data in France reveal high heterogeneity between regions (ENETWILD-consortium et al., 2021; Guberti et al., 2019), data collected at hunting grounds on the number of harvested animals, alongside with the scarcity of hunters, and the increasing human-wildlife conflicts suggest that hunting game are not sufficient to limit wild boar populations and their dispersal to unexpected areas (Jori et al., 2021; Keuling et al., 2010; Massei et al., 2014). The increasing wild boar population is an important risk factor for introduction, spread, and settlement of ASF in France, as proven in several exposed countries (Boklund et al., 2020; Guberti et al., 2019; Oļševskis et al., 2016).

When simulating the ASF epidemics, after viral seeding, given the wild boars' susceptibility to the virus and its high lethality, wild boar populations at both regions were drastically impacted, leading to an important population decrease. These results are in agreement with other epidemiological studies in ASF-affected areas where wild boars were depleted during the ASF epidemic phase (Guberti et al., 2019; Mačiulskis et al., 2020; Viltrop et al., 2021). Although wild boar mortality in ASF-affected regions is also increased due to depopulation strategies, serological studies and experimental ASF infections suggest that only a small proportion of infected wild boars survive and overcome the disease with the current genotype 2 strain circulating in Europe (Guberti et al., 2019; Martínez-Avilés et al., 2020; Morelle et al., 2020; Oļševskis et al., 2020).

Despite sharing a common trend of population dynamics, the transmission patterns were significantly different in the two study areas. When excluding hunting, the wild boar population established in the DPA was heavily impacted by ASF during the first years of the epidemic. Nevertheless, by the end of the epidemic phase a repopulation took place over the last 2 years of simulation. This repopulation process could be a result of the disease fading-out (year 1.6 post-introduction) due to a lack of availability of contact with new susceptible individuals to maintain ASFV circulation. In contrast, in the area close to the Belgian border the transmission process proceeded slower, affecting to a lower extent the global population in the first years after ASF introduction. This allowed a yearly renewal of the pool of susceptible individuals, significantly lengthening the epidemic duration. Here, the disease fade-out occurred after 2.6 years post-introduction, leading to a gradual growth of the population. Although it did not recover to its initial level, the trend in the model revealed a wild boar population that suggests it would eventually recover to its initial density.

The landscape fragmentation was highlighted as an important ecological factor that influences ASF spread and evolution. For instance, a uniform ASF dynamic (reflected in the number of infected individuals and carcasses) can be seen in the non-fragmented landscape (DPA), in

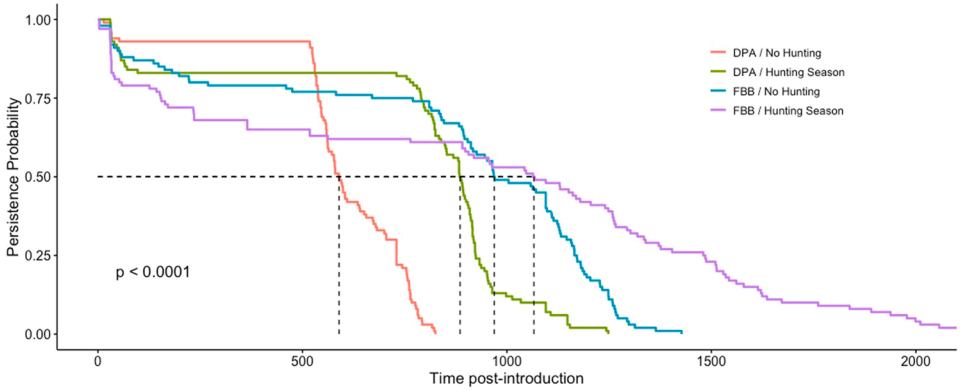


Fig. 6. Epidemic duration analysis. Duration of the epidemic of the four scenarios. The representation of the ASF outbreak in *Pyrénées-Atlantiques* department when excluding hunting is depicted in red and when including hunting, in green. The Franco-Belgian border epidemic duration is depicted in blue when excluding hunting and in purple when including hunting activities. The duration is expressed in days. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

contrast to the results of the fragmented landscape (FBB). In contrast to the number of infections, the shorter duration of the epidemic in the homogeneous landscape could be explained by the higher contact probability among individuals due to the connection between pixels, accelerating the transmission and disease course. These observations match with other studies that predicted the highly dense forest areas and woodlands as risk factors for ASF outbreaks (Podgorski et al., 2019; Virgós, 2011) where additionally, wild boar depopulation and carcass removal may be challenging, favoring ASF maintenance. Furthermore, fragmented habitat with unsuitable areas for wild boars, was shown to limit wild boar movements, hence reducing the probability of introduction as well as ASFV expansion across the landscape. One control strategy in ASF-affected countries, is to artificially fragment the landscape by fencing areas of interest and creating zones, in order to limit wild boar movement and hence further ASF spread (Dixon et al., 2020; Jo and Gortázar, 2020). Such strategy, along with other control measures (e.g., definition of core-infected and surveillance zones, active carcass search and removal, limitation of forestry activities and wild boar depopulation), succeeded in ASF eradication in Czech Republic and Belgium (Dellicour et al., 2020; Marcon et al., 2019), which were declared free from ASF in 2019 and 2020, respectively (OIE, 2020, 2019). These control measures must be implemented in conjunction as soon as ASF is detected for eradication.

In this study, the lack of connectivity on landscape was also reflected in a less effective transmission and lower number of infected carcasses. It is important to note that, although there was a lower number of infections, the duration of the epidemic is much larger in the fragmented landscape than the homogeneous habitat. Currently, only few studies have linked habitat fragmentation as a factor of ASF occurrence/spread risk (Huang et al., 2017; Podgorski et al., 2019). Understanding the habitat structure as an important factor affecting ASF dynamics remains limited. More research is necessary to elucidate the link between the landscape and the disease dynamics to deliver better surveillance and intervention strategies. This study accounted for seasonality to represent carcass persistence in the environment. Seasonal patterns could also impact the population dynamics and movements. For instance, seasonal mast tree production and other resources could be a driver for wild boar direction movements and offspring could differ according to the favorable and unfavorable conditions. Nonetheless, these factors would increase the model complexity and require additional parameters. Future research should include more complex factors such as spatio-temporal variation on food resource availability for the wild boar population that could reflect a more realistic scenario. At the same time, obtaining good-quality and up-to-date data for the model building could be challenging.

Depopulation or intensive hunting is an ASF-control strategy recommended by the European Commission and mandated by the EU legislation to lower wild boar density and limit ASF spread (Guberti et al., 2019; Jo and Gortázar, 2020; Mačiulskis et al., 2020; Viltrop et al., 2021). Here, hunting activities were not implemented as a control strategy but as seasonal hunting game. These activities impacted directly ASF dynamics. When comparing with the non-hunting scenarios, the number of infections and infected carcasses are significantly lower, regardless of the study area. A series of infection waves appeared to happen each year, especially in the fragmented area. These peak waves could be explained by the group dispersion triggered by hunting activities. Several human activities can provoke wild boar group displacement, especially when hunting using dogs (Scillitani et al., 2010). These group translocations can increase the probability of ASF transmission and spread. Similarly, it is important to notice that the epidemic duration of the hunting-including scenarios was significantly lengthened. For instance, the disease faded-out after 2.8 years post-introduction in the FBB area and after 2.3 years post-introduction in the DPA area. An enzootic persistence can be seen until the end of the 8-year simulation in some iterations. Currently, wild boar population reduction does not seem to stop ASF spread in regions like Latvia (Schulz et al., 2019) and Poland (European Food Safety Authority (EFSA) et al., 2017). A sustained and on-going wild boar population reduction at national levels requires tremendous economic effort and interdisciplinary workforce. While wild boar extermination seems unrealistic and expensive, depleted areas would be repopulated eventually after stopping the intensive hunting (Guberti et al., 2019), as shown in the results of the model. Thus, a continuous hunting strategy may be essential for regulating the local wild boar population. For instance, Belgian authorities prohibited forestry activities (including hunting game), limited dispersal of infected wild boars by fencing affected areas, and impairing movements from the infected zone. Finally, when an area was closed, a depopulation strategy was carried out. The conjunction of all these control measures implemented in time was essential for ASF eradication.

It is important to increase surveillance for rapid detection, and rapid control implementation (i.e., fencing in the early stages before epidemic peak) and identify gaps in depopulation strategies. Should an ASF outbreak happen, reactivity needs to be optimal (Lange and Thulke, 2015). Hunting efforts must include professional hunting rather than solely seasonal hunting to achieve acceptable wild boar population densities. Collaborations between professional hunters, hunting associations, and scientists are desirable for acquiring objective data and monitoring wildlife while performing ASF passive surveillance (Cretois et al., 2020; Urner et al., 2021). For instance, hunted wild boars should be sampled and tested with PCR and serology tests since results could be very important for determining ASF epidemic status of regional wild boar populations (Martínez-Avilés et al., 2020). Because of the unknown mechanisms of transmission within wildlife and between wild and domestic compartments, there is a lack of data and modelling research on unraveling this interface and it still needs to be represented (Hayes et al., 2021).

Finally, risks for ASF spread during depopulation strategies must be considered, as contamination by infected blood during depopulation strategies could contribute to further spread of the ASFV in the environment through hunting equipment (Chenais et al., 2019; Guberti et al., 2019). This poses an important risk to domestic pig producers, which potentially offer a pool of alternative susceptible hosts, especially to outdoor farms, and directly shapes the outcome of this disease. ASF is considered a global issue and it is essential that international authorities collaborate to delimit both risk areas and control strategies. These control measures must be implemented in conjunction considering the landscape characteristics (i.e., habitat fragmentation, land-use, etc.), and existing forestry activities (i.e., hunting activities).

5. Conclusion

This study accounted for the natural disease progression of ASF in restricted areas representing wild boars, assuming a single introduction location, and without implementation of control strategies. This model included specific landscape characteristics for each study area and a yearly hunting activity, in order to be closer to the reality and to show their importance in ASF course. Through result comparison among the two areas, this study highlighted a strong impact on the fragmentation of the territory on the ASF propagation. On the other hand, hunting activities induces a considerably lengthening of the epizootic duration, leading to enzootic situations in some iterations and increasing the risk for transmission to the domestic sector. The results of this study provided information on the definition and implementation of control measures in case of ASF incursion. The area delimitation with implementation of fences induces an artificial landscape fragmentation which is an important control measure for ASF outbreaks. This model has the flexibility to be adapted to different regions worldwide to show high-risk areas for ASF establishment and spread. Additionally, this model requires forest cover data as input parameter and can be promptly adapted to a specific scenario. Further complex models need to be addressed to represent control strategies during outbreaks, (i.e., fence implementation, depopulation strategies, and carcass removal) and compare

outcomes with different reactivity scenarios. These results would provide an opportunity to sustainably manage wildlife and analyze the infection process, since it remains a real challenge for ASF epidemiology.

Conflict of Interest

The authors of this manuscript (Luis G. Salazar, Nicolas Rose, Brandon H. Hayes, Pachka Hammami, Eric Baubet, Stephanie Desvaux, and Mathieu Andraud) certify that they have NO affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

Acknowledgements

The authors are indebt to the Direction Générale de l'Alimentation (DGAI) of the French Ministry of Agriculture for financial support.

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