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The African swine fever modelling challenge: Model comparison and lessons learnt

Pauline Ezanno^{a,*}, Sébastien Picault^a, Servane Bareille^{a,b}, Gaël Beaunée^a, Gert Jan Boender^c, Emmanuelle A. Dankwa^d, François Deslandes^e, Christl A. Donnelly^{d,f}, Thomas J. Hagenaars^c, Sarah Hayes^f, Ferran Jori^g, Sébastien Lambert^{h,1}, Matthieu Mancini^{a,b}, Facundo Munoz^g, David R.J. Pleydell^g, Robin N. Thompsonⁱ, Elisabeta Vergu^e, Matthieu Vignes^j, Timothée Vergne^b

^a INRAE, Oniris, BIOEPAR, 44300 Nantes, France

^b INRAE, ENVT, IHAP, Toulouse, France

^c Wageningen Bioveterinary Research, Lelystad, the Netherlands

^d Department of Statistics, University of Oxford, Oxford, United Kingdom

^e Université Paris-Saclay, INRAE, MaIAGE, 78350 Jouy-en-Josas, France

^f Department of Infectious Disease Epidemiology, Faculty of Medicine, School of Public Health, Imperial College London, United Kingdom

^g CIRAD, INRAE, Université de Montpellier, ASTRE, 34398 Montpellier, France

^h Centre for Emerging, Endemic and Exotic Diseases, Department of Pathobiology and Population Sciences, Royal Veterinary College, University of London, United Kingdom

ⁱ Mathematics Institute and Zeeman Institute for Systems Biology and Infectious Disease Epidemiology Research, University of Warwick, Coventry, United Kingdom

^j School of Mathematical and Computational Sciences, Massey University, Palmerston North, New Zealand

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ABSTRACT

Robust epidemiological knowledge and predictive modelling tools are needed to address challenging objectives, such as: understanding epidemic drivers; forecasting epidemics; and prioritising control measures. Often, multiple modelling approaches can be used during an epidemic to support effective decision making in a timely manner. Modelling challenges contribute to understanding the pros and cons of different approaches and to fostering technical dialogue between modellers. In this paper, we present the results of the first modelling challenge in animal health – the ASF Challenge – which focused on a synthetic epidemic of African swine fever (ASF) on an island. The modelling approaches proposed by five independent international teams were compared. We assessed their ability to predict temporal and spatial epidemic expansion at the interface between domestic pigs and wild boar, and to prioritise a limited number of alternative interventions. We also compared their qualitative and quantitative spatio-temporal predictions over the first two one-month projection phases of the challenge. Top-performing models in predicting the ASF epidemic differed according to the challenge phase, host species, and in predicting spatial or temporal dynamics. Ensemble models built using all team-predictions outperformed any individual model in at least one phase. The ASF Challenge demonstrated that accounting for the interface between livestock and wildlife is key to increasing our effectiveness in controlling emerging animal diseases, and contributed to improving the readiness of the scientific community to face future ASF epidemics. Finally, we discuss the lessons learnt from model comparison to guide decision making.

1. Introduction

Mathematical epidemiological models are key decision support systems for policy and decision making in public health, as recently

illustrated by the SARS-CoV-2 pandemic (McCabe and Donnelly, 2021; James et al., 2021), but also in animal health, with key examples on regulated diseases such as foot-and-mouth disease (Ferguson et al., 2001; Kao, 2002; Keeling et al., 2001; Probert et al., 2016), avian

* Corresponding author.

E-mail address: pauline.ezanno@inrae.fr (P. Ezanno).

¹ Present address: Université de Toulouse, INRAE, ENVT, IHAP, Toulouse, France.

influenza (Andronico et al., 2019; Benincà et al., 2020; Stegeman et al., 2010), African swine fever (ASF; Hayes et al., 2021; Lange and Thulke, 2017; Yoo et al., 2021), as well as on endemic diseases (Ezanno et al., 2020). Solid epidemiological knowledge and predictive modelling tools are required to fulfil challenging objectives, including: understanding epidemic drivers, forecasting epidemics and prioritising control measures. However, disentangling which modelling approaches best support decision making is a sensitive task. Favouring a first-choice approach, without fully assessing the behaviour of the model and its predictive ability is a common pitfall (Kao, 2002). In addition, models that fit reported epidemic data well potentially fail at adapting to the wide range of possible intervention scenarios, while models capable of comparing various control strategies often are too complex for their many parameters to be estimated accurately and precisely. Moreover, when modelling during an epidemic, data availability may be limited, especially early in the epidemic. Therefore, there is a crucial need to fill knowledge gaps in our understanding of the pros and cons of different approaches under various outbreak and data availability scenarios.

Modelling challenges can help to address such issues by providing a controlled and standardised environment, as has been highlighted in public health where such challenges have been organised for seasonal flu (Viboud and Vespignani, 2019), Ebola (Viboud et al., 2018) and vector-borne diseases (Del Valle et al., 2018; Johansson et al., 2019). These competitions were organised for specific infectious diseases. They aimed to improve the ability of the scientific community to make judicious use of models for forecasting epidemics. The basic idea behind such challenges is to go beyond traditional competing settings. They are avenues to open the door to international collaborations, or even cooperation, by making the best out of incomplete data and knowledge on the transmission dynamics and highlighting other remaining uncertainties and priorities. In addition, multi-model analyses allow the exploration of the performance of ensemble models. Given that the predictions of individual models generally differ, basing a management decision on the results of a single model is risky and may not be the most robust approach (Probert et al., 2016). Considering all models together in ensemble models can lead to more robust predictions, thereby reducing the risk taken by decision makers, so long as a sufficient number of models are included (Webb et al., 2017). This property is known as “collective intelligence”. Examples of successful multi-model analyses include: forecasting seasonal flu dynamics in the USA (Reich et al., 2019); simulating Ebola outbreaks resembling those of West Africa (Viboud et al., 2018); guiding decision-making for foot-and-mouth disease control (Probert et al., 2016); and also very different frameworks such as weather forecasting (Leutbecher and Palmer, 2008), protein 3D structure prediction (Jamroz et al., 2016), and gene regulatory network reconstruction (MARBACH et al., 2012).

In epidemiology, such modelling challenges have so far only addressed public health problems. However, beyond generic model structures and inference methods shared within the epidemiological modelling framework irrespective of the application, infectious diseases involving animals raise specific issues. An important issue is that several host species may be involved, and these hosts may exhibit specific mobility patterns as well as heterogeneous spatial distributions. In addition, control measures used to prevent the spread of animal diseases (e.g., fencing, test-and-culling, preventive culling) largely differ from those used in public health, and might need specific modelling approaches to be accounted for, as demonstrated in the comparison made between different models developed to assess intervention to control foot-and-mouth disease (Probert et al., 2016; Webb et al., 2017). Such key features for animal diseases were, by definition, not considered in previous modelling challenges, highlighting the need for specific challenges dedicated to animal health.

The current African swine fever (ASF) pandemic (2007 – today) provides a perfect context to develop the first modelling challenge in animal health. ASF is an emerging animal disease that spreads in Europe and Asia at the interface between domestic pigs and their various

wildlife counterparts (Sánchez-Cordón et al., 2019). Due to the high mortality rate and the drastic control measures that have to be implemented, ASF and its control have a large global impact on animal health and welfare, farmer livelihoods, food security and the economy of the livestock sector (Dixon et al., 2020). ASF also threatens biodiversity of wild suids in certain regions of the world (Luskin et al., 2021). The virus spreads internationally because of human and animal mobility, making ASF a major threat for most countries with a swine industry (Vergne et al., 2017).

To enhance the ability of modellers to advise policy makers in a timely manner and promote international collaboration, we have organised the first modelling challenge in animal health (ASF Challenge), using synthetic data from an ASF epidemic simulated at the interface between domestic pigs and wild boar in an industrial farming context similar to western Europe (Picault et al., 2022). The five teams that succeeded in completing the competition were asked to develop a model to fit the synthetic data at three different stages of the epidemic, to predict the spatio-temporal development of the epidemic and to assess the effectiveness of a limited number of management strategies. The approaches developed by four of the five teams are described in dedicated papers of this special issue (Muñoz et al., 2022; Beaunée et al., 2022; Dankwa et al., 2022; Han and Vignes, 2022).

In this paper, we compare the modelling approaches proposed by the five independent international teams. We assess their ability to predict the temporal and spatial epidemic spread and to rank the proposed alternative control strategies. From these models, we built different ensemble models (for temporal and spatial predictions), whose performance is compared to each team’s model. Finally, we discuss the lessons learnt from this model comparison, to guide decision making and improve our preparedness to face real ASF epidemics.

2. Methods

2.1. Brief overview of the ASF Challenge

The ASF Challenge was launched on 27 August 2020 and lasted until 13 January 2021. A new mechanistic stochastic metapopulation and multi-host spatial model of ASF transmission (named model M0 hereafter) was used to generate synthetic data mimicking an ASF-like epidemic detected at the interface between pig farms and wild boar in an isolated territory (an island) representative of a south-western European context with regards to livestock and wildlife interactions (Picault et al., 2022). Land use, size and location of farms, trade movement between farms, as well as wild boar hunting bags per administrative unit (the best available data related to actual wild boar densities) were either derived from real French data in two adjacent administrative regions (Occitanie and Auvergne-Rhône-Alpes), or simulated (details available in Picault et al., 2022). These were used as input data in model M0 to produce a single synthetic epidemic, and were also provided to the modelling teams. The ASF-like epidemic was chosen on the basis of the following selection criteria (none of which were communicated to participating teams). The selected epidemic had the characteristics that data collection started after a first outbreak had been reported in a domestic pig farm, in the vicinity of a forest area and less than 200 days after the introduction of the virus in wild boar. Such a situation was assumed to be both realistic and to lead to a (at least partially) manageable epidemic. A further selection criteria was that more than 250 wild boar were to be infected (but not detected) when the disease was first reported so that the epidemic did not spontaneously fade-out. Thus, the observed epidemic had to last for more than 100 days, with a progressive diffusion through a forest area with a high density of wild boar and an apparently successful control of the disease (i.e., decrease in the number of detected cases) by the end of the ASF Challenge. ASF incidence data (detected cases) for both pig farms and wild boar were provided to the modelling teams while the epidemic developed, dividing the challenge into three phases, which started 50, 80 and 110 days after

the first detection, respectively. Detection of cases was not perfect, its sensitivity varying between host populations and over time (Picault et al., 2022).

At the start of the challenge, three presentations were made: (1) to give information on ASF, the concerned area, and ASF control; (2) to describe the provided data; and (3) to outline the challenge rules (SI1–3). In addition to this initial information session, teams could ask questions on a shared platform (<https://app.slack.com>), and of course had access to published literature via their own initiative. At the beginning of each phase, the ASF Challenge teams were provided with identical surveillance outputs and an identical situation report. The objectives for challenge teams were to model the dynamics of the selected synthetic epidemic assuming a set of control strategies, predict the expansion of the epidemic and prioritise a set of defined alternative interventions. This is described in more detail in Picault et al., 2022.

2.2. Qualitative and quantitative comparison of teams' approaches and predictions

First, we qualitatively compared the modelling approaches proposed by each team. This comparison was helpful for highlighting the diversity, and similarity, of approaches used to predict ASF virus spread under various control scenarios. As teams were free to choose their own approach and the format in which they provided their feedback to the challenge organisers, this step was also useful for characterising teams' model outputs and identifying what was comparable between them. At the end of the challenge, all teams were asked to describe their models in detail using a common template, and to make a video presenting their modelling assumptions to other teams and to the organisers. Hereafter, we describe how teams modelled transmission within each host species, the epidemiological unit chosen for each species, the way they coped with the interface between wild boar populations and pig farms and its consequence on ASF virus transmission at large scale, and finally the spatial units chosen. We also describe the format chosen by teams to provide us feedback.

Second, we compared the performance of team models to predict the synthetic temporal spread of ASF virus, over the different challenge phases. More specifically, we assessed how close their predictions were to the selected synthetic data produced by model M0 when all the assumptions made for the "observed" period were fixed and maintained throughout the prediction period (e.g., no alternative or additional control measures). We relied on predictions from each repetition r of team model k of the cumulative number of detected pig farm outbreaks, $PF_k(t, r)$, and the cumulative number of detected wild boar cases, $WB_k(t, r)$ as key outputs. For each of these two variables, we compared the median provided by each team and the 80% credibility intervals (i.e., 10th to 90th percentiles) when available, to the predictions of model M0.

Third, we compared spatial predictions arising from the models produced by the challenge teams. Based on their outcomes, we summarised spatial predictions for detected outbreaks in pig farms. We calculated the probability of detecting ASF at a given farm as the proportion of stochastic repetitions in which it was the case. To quantitatively compare predictions, we built, for each team's model k , a detection index, D_k , calculated as the proportion of pig farms (among a total of N_{PF} farms) predicted to be detected as infected with a probability p_i^k higher than a cut-off value, c , given that they were truly detected as infected (i.e., farm i belong to \mathcal{D} , the ensemble of detected infected farms) in the selected synthetic trajectory of model M0 (Eq. (1)). For team k , the probability p_i^k of ASF being detected on farm i was calculated as the number of repetitions in which this was the case over the total number of repetitions performed by team k . This helped identify which team models were able to predict the location of detected infected farms with high accuracy. Considering the stochasticity of infection events and the radius used in the definition of the surveillance zone (a 15-km-radius

area with an elevated probability of detection), we also allowed for a tolerance in location predictions to assess the abilities of models to predict spatial hotspots or risk areas. Hence, predictions of detected ASF infections on pig farms were classified as correct if those farms were located within 15 km from a farm that was detected as infected in model M0. For wild boar, team k predicted the probability of detecting infected spatial unit s , p_s^k , calculated as the number of repetitions in which the spatial unit s was detected as infected over the total number of repetitions performed by team k . Since various spatial scales (i.e., tile sizes) were used by teams to model infection dynamics in wild boar, spatial predictions of these dynamics were compared visually.

$$D_k = \sum_{i=1}^{i=N_{PF}} (p_i^k \geq c \& i \in \mathcal{D}) / N_{PF} \quad (1)$$

Fourth, we built ensemble models, separately for each combination of (1) temporal or spatial dynamics, and (2) pig farms or wild boar hosts. For temporal forecasts, we built the following two ensemble models for detecting ASF (1) on pig farms, and (2) among wild boar:

- the mean of the expected values predicted by each team at each time t , i.e., $\sum_{k \in \mathcal{T}} (PF_k(t)) / N_{\mathcal{T}}$ and $\sum_{k \in \mathcal{T}} (WB_k(t)) / N_{\mathcal{T}}$, with $X_k(t) = \bar{X}_k(t, r)$, $X \in \{PF, WB\}$ and $N_{\mathcal{T}}$ the number of teams having produced the used output;
- the worst-case predictions at each time t , i.e., the highest number of detected cases among the expected values predicted by teams: $\max(PF_k(t))$ and $\max(WB_k(t))$.

For spatial predictions, we first recalculated, per team, the probability to detect ASF among wild boar in a given infected spatial unit, utilising the spatial unit of model M0 (squares of 25 km²) to ease comparisons with the selected synthetic data. For teams that used a larger spatial unit, we assumed that the detection probability was uniform across the whole unit, thus we attributed the same value to all sub-units with centroids contained within the larger unit. For teams that used a smaller spatial unit, we assumed the tile was detected as soon as part of it was. We then built the four following ensemble models:

- the mean of teams' predicted expected values for the probability of detecting ASF on pig farm i , i.e., $\sum_{k \in \mathcal{T}} p_i^k / N_{\mathcal{T}}$ and, for wild boar, of detecting ASF within spatial unit s , i.e., $\sum_{k \in \mathcal{T}} p_s^k / N_{\mathcal{T}}$;
- the worst-case predictions at each time t , i.e., the highest predicted probability of detecting ASF: $\max(p_i^k)$ and $\max(p_s^k)$;
- the weighted average, where the weight w_k for team k equals the number of repetitions performed by team k : $\sum_{k \in \mathcal{T}} p_i^k w_k / N_{\mathcal{T}}$ and $\sum_{k \in \mathcal{T}} p_s^k w_k / N_{\mathcal{T}}$;
- the threshold-average, defined as the mean of teams' prediction unless one or more teams predicted a probability higher than a threshold c , in which case the highest of these probabilities was used: $\max(\max(p_x^k | p_x^k \geq c)_{k \in \mathcal{T}}, \sum_{k \in \mathcal{T}} p_x^k / N_{\mathcal{T}})$, $x \in \{i, s\}$. Threshold-average ensemble models are hybrid models that aim to share the properties of average and worst-case ensemble models. Three values were used for the probability threshold c : 0.5, 0.7, and 0.9, with 0.9 corresponding to the most precise, but least sensitive detection threshold, and 0.5 being the least precise, but the most sensitive detection threshold.

Finally, we compared team predictions for the effectiveness of the various control measures assessed in addition to regulated measures. In phase 1, teams were asked to assess the effectiveness of implementing fences around the forest near the first detected case, combined (or not) with intensive hunting of wild boar. In phase 2, teams were asked to assess the effectiveness of five alternative measures: (1) depopulating pig farms located less than 3 km from a known infected pig farm (this area was a protection zone); (2) depopulating pig farms known to have

had contact with an infected pig farm within the three weeks prior to detection; (3) depopulating pig farms located less than 3 km away from a known infected wild boar carcass; (4) extending the surveillance zone radius from 10 km to 15 km; and (5) extending the radius of the area of active search around found wild boar infected carcasses from 1 km to 2 km (see [Picault et al., 2022](#)). To assess the effectiveness of each measure, we calculated the differences between the predicted results with and without the implementation of each measure within the same model, and then compared the absolute and relative differences obtained by the teams that tested the measures.

2.3. Feedback from the participants

Following completion of the ASF Challenge, a series of internal workshops were organised to collectively gain knowledge on the approaches used by each team and most importantly to obtain feedback from the teams on several topics. An online feedback questionnaire was administered to the participants to investigate several questions related to the relevance of the data and documents provided before and during the challenge, the feasibility of the challenge in relation to the time available, the skills used or missing in the modelling teams, the organisation of the challenge itself, and the knowledge gained by teams during the ASF Challenge.

3. Results

3.1. Qualitative comparison of the teams' approaches

All teams used stochastic compartmental models. All but one team took this approach for both host species (wild boar and pigs; [Table 1](#)). In one case, the risk of infection on pig farms was estimated independently from simulations of spread among wild boar and was modelled using a probabilistic approach (CIRAD, [Muñoz et al., 2022](#)). The dynamics of the two host populations were either described by two distinct models (three teams), or as a single model (two teams). In addition, most teams chose similar epidemiological units. In all but one team, wild boar hosts were modelled individually. The WUR team was the only team to not consider individual animals, choosing instead to use several animals located in a given spatial area as a basic epidemiological unit. In all but one team, infection status in pig farms was defined at farm scale. The UK team however defined the health status of individual pigs within farms ([Dankwa et al., 2022](#)). Finally, all teams modelled both the temporal and the spatial infection dynamics. Most models were in discrete time with a time step of one day, except the INRAE and CIRAD models, which used continuous time for at least one of the two modules (pig farms or wild boar). The chosen spatial units and shapes for modelling transmission

among wild boar largely differed among teams. Two teams used hexagons, two teams used squares, and one team used rectangles. Moreover, these units ranged from very small (1 km²) to very large (195 km²) tiles. Most teams provided outputs at the individual scale (i.e., a single wild boar or pig farm), except the WUR team, who's outputs indicated the presence or absence of ASF within small patches. The role of the spatial unit was difficult to assess as none of the teams has tested different units. UK and Massey teams have chosen tile size according to the typical home range size for wild boar, with the force of infection due to wild boar being defined per tile. The UK team also accounted for a maximum infection range for transmission between tiles, which was not the case in the Massey model in which transmission occurred within tiles. The WUR team chose a much smaller unit, inspired by [Hayama et al. \(2020\)](#) who estimated the classical swine fever infection risk for pig farms located in infected wild boar areas. Finally, the CIRAD and INRAE teams chose much larger spatial units, for reducing computing times while keeping sufficient resolution for characterising spatial heterogeneity (e.g., a 5-km distance between centroids of neighbouring tiles in the CIRAD model). As the units chosen were large compared to the vital domain of wild boar, a simplifying hypothesis was made that transmission only took place with directly neighbouring tiles. Such modelling choices especially impacted the inference of model parameters, as well as carcass discovery.

With regards to virus transmission, heterogeneity arose in the choices made by teams for modelling transmission between wild boar and pig farms: the CIRAD team did not link their models for the two host species and simply modelled risk in pig farms as a function of smoothed wild boar case data ([Muñoz et al., 2022](#)); the UK ([Dankwa et al., 2022](#)) and the WUR teams modelled the force of infection from wild boar to pig farms but not from pig farms to wild boar as they found no strong evidence, based on the synthetic data provided, of transmission from pig farms to wild boar; finally, the INRAE ([Beaunée et al., 2022](#)) and Massey ([Han and Vignes, 2022](#)) teams defined a force of infection in both directions, from wild boar to pig farms and from pig farms to wild boar. Assuming no transmission from pigs to wild boar (three teams) implies that control measures targeting pig farms had, by definition, no impact on wild boar. Also, pig farms can get infected by other transmission pathways: proximity to other farms (CIRAD, UK and INRAE teams) and by animal trade movements between farms (all but WUR team). Due to the limited number of pig farm outbreaks and the dominant role of boar-to-farm transmission in disease introduction into pig farms, the power of data was considered insufficient by the WUR team for estimating a non-zero between-farm transmission kernel ([Boender et al., 2014](#)). Trade movements of pigs were generally modelled based on the historical data that were provided to teams, except the UK team who used historical data for observed period and fitted exponential random

Table 1

Main team-model characteristics. Modelling approaches and epidemiological units for wild boar (WB) and pig farm (PF) components, transmission assumptions at the interface between WB and PF, and the spatial units adopted by each team during the ASF Challenge.

Team	Wild boar (WB)			Pig farms (PF)		Number of models	Interface WB / PF
	Approach	Epid. unit	Spatial unit	Approach	Epid. unit		
CIRAD ^a	SCM ^b	Individual	Hexagon (86.6 km ²)	Probability	Farm	2	WB to PF ^c
UK ^d	SCM	Individual	Rectangle (7.5 km ²)	SCM	Individual	2	WB to PF
INRAE ^e	SCM	Individual	Hexagon (195 km ²)	SCM	Farm	2	Both directions
Massey ^f	SCM	Individual	Square (10 km ²)	SCM	Farm	1	Both directions
WUR	SCM	Spatial area	Square (1 km ²)	SCM	Farm	1	WB to PF

^a [Muñoz et al., 2022](#).

^b SCM: stochastic compartmental model.

^c Link made via smoothing of observed cases, not via stochastic model output.

^d [Dankwa et al., 2022](#).

^e [Beaunée et al., 2022](#).

^f [Han and Vignes, 2022](#).

graph model (ERGM) to historical data to predict future movements. No team explicitly simulated wild boar movements, nor how movement patterns could be affected by intensive hunting. To model transmission between two distant epidemiological units, some teams (UK, WUR, and, for transmission via fomites, CIRAD teams) used distance-based kernels whilst others assumed (for speed) that the virus could only move to adjoining tiles and no further (INRAE, Massey and, for wild boar, CIRAD teams). A speed limit for between-boar transmission of no more than (approximately) 10 km per day was adopted by most teams, with some models imposing a maximum distance and some not. Such a speed limit is in agreement with estimates of spatial spread due to wild boar territoriality which informed the construction of model M0 (Froehly et al., 2020).

To calibrate their models, teams used various inference approaches. The fastest methods corresponded to optimisation methods (INRAE, Massey, and WUR teams): likelihood maximisation, Jaccard index maximisation, and least squares minimisation. Bayesian methods, although more demanding in terms of computing time, were also used (UK and CIRAD teams): Markov chain Monte Carlo (MCMC) and Approximate Bayesian Computation (ABC). To increase the speed of their analyses, these two teams (CIRAD and UK teams) restricted their models to the part of the island where infection had been detected.

Teams were requested by the organisers to provide information about their models at various stages during the challenge. First, teams were asked for a textual description of their predictions, to ease qualitative comparisons. Second, teams were asked to provide the organisers with quantitative model predictions that should be “as precise as possible”. Teams were free to choose the epidemiological unit, the spatial unit and the format that they desired for submitting their predictions. As a result, a large variety of output types was received, which made comparisons somewhat difficult. With regards to file format, most teams chose the csv format, also some teams also provided data in Rdata files. Some teams provided output means and confidence intervals, others provided full details of every stochastic repetition. Some provided aggregated outputs, others provided the exact time and/or location of case detection. Finally, some teams provided code for simulating with their models, and/or, for visualising their model outputs.

3.2. Model ability to forecast the temporal dynamics over four weeks

Phases 1 and 2 of the challenge exhibited the largest changes in the number of detected cases in both pig farms and wild boar. As such, they were the most interesting phases for comparing temporal forecasts, thus, we focus on these phases in the subsequent analyses.

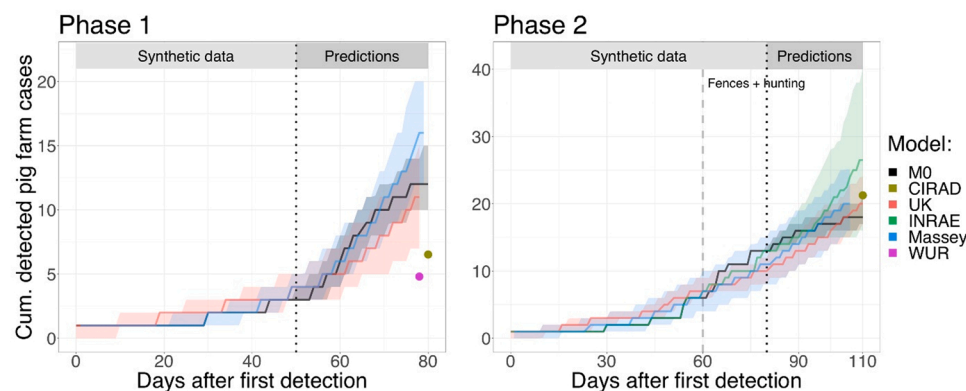


Fig. 1. Predicted cumulative numbers (line: median; shaded area: 10th to 90th percentiles) of detected infected pig farms according to teams’ models, between days 50 and 80 (“Phase 1”) or between days 80 and 110 (“Phase 2”). The dotted line delimits the prediction period for each phase of the challenge. The dashed line shows when fences were implemented and intensive hunting started. Projections assumed similar control measures during the prediction period and the observed period. Model M0 was used to produce synthetic data up to the beginning of the prediction period (using the stochastic repeat selected for the challenge – black line in the figure), then 500 stochastic repetitions were run to show possible variability over the prediction period. No values were provided by INRAE team for phase 1, nor from WUR team for phase 2. No variability

was provided by WUR and CIRAD teams for these outputs.

3.2.1. Detected pig farm cases

Most teams provided very good forecasts of the cumulative incidence of detected infected pig farms (Fig. 1). They fixed control measures for the duration of the prediction period, assuming measures remained similar to those of the observed period, i.e., for phase 1: regulatory measures only; for phase 2: fences installed 60 days after the detection of the first case and intensive hunting within the fenced area and a 15-km buffer around it. See teams’ papers for more details (Muñoz et al., 2022; Beaunée et al., 2022; Dankwa et al., 2022; Han and Vignes, 2022). To compare their predictions to the dynamics that could have been observed with model M0 under these conditions, we ran 500 stochastic repetitions keeping control measures similar to just before the prediction period (i.e., measures already implemented on day 50 for predictions during phase 1, and on day 80 for predictions during phase 2; Fig. 1). Complementary scenarios were also examined by the teams (see companion papers of the special issue), but their heterogeneity made them difficult to compare.

3.2.2. Detected wild boar infections

The temporal dynamics of detected wild boar cases appeared more difficult to predict (Fig. 2). First, the heterogeneity in model predictions was much greater than for pig farms. Second, the biases associated with model predictions were not the same from one phase to the other: during phase 1, most models tended to underestimate the incidence of detected wild boar infections, whereas most models tended to overestimate it during phase 2. The difficulty in phase 2 was to represent the installation of fences and the intensive hunting within the fenced area and in the 15-km-radius buffer zone around the fences. Bayesian approaches (UK and CIRAD teams) outperformed other methods here (Fig. 2, Phase 2). The UK team also selected simulations whose epidemic amplitude was in agreement with the selected synthetic data from model M0 at the end of the observation period, while other teams started their predictions from the day of first detection.

Ensemble models can generate leverage from heterogeneous model predictions. Fig. 3 presents the two ensemble models for temporal predictions: an average of all team-predictions and a worst-case ensemble taking the largest number of detected wild boar cases among all team-predictions. The top-performing ensemble model (i.e., the closest to model M0 predictions) was not the same in phase 1 (worst-case) and in phase 2 (average).

3.3. Model ability to predict the spatial spread of ASF

Concerning spatial predictions, the most interesting challenge phases were phase 1 for pig farms (initial ASF spread) and phase 2 for wild boar (once fences had been implemented). Thus, we focused our analyses on

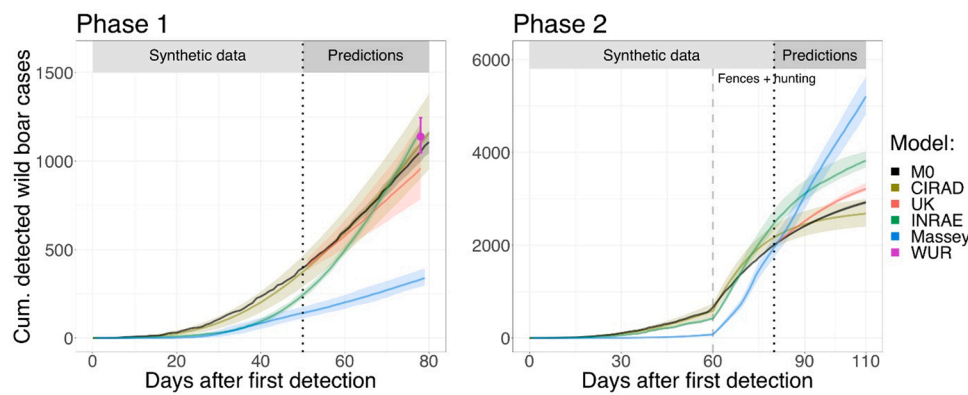


Fig. 2. Predicted cumulative numbers (line: median; shaded area: 10th to 90th percentiles) of detected infected wild boar according to teams' models, between days 50 and 80 ("Phase 1"), and between days 80 and 110 ("Phase 2"). The dotted line delimits the prediction period for each phase of the challenge. The dashed line shows when fences were implemented and intensive hunting started. Projections assumed similar control measures during the prediction period and the observed period. Model M0 was used to produce synthetic data up to the beginning of the prediction period (using the stochastic repeat selected for the challenge), then 500 stochastic repetitions were simulated to show possible variability over the prediction period (very low during Phase 2). No values were provided from the WUR team for phase 2.

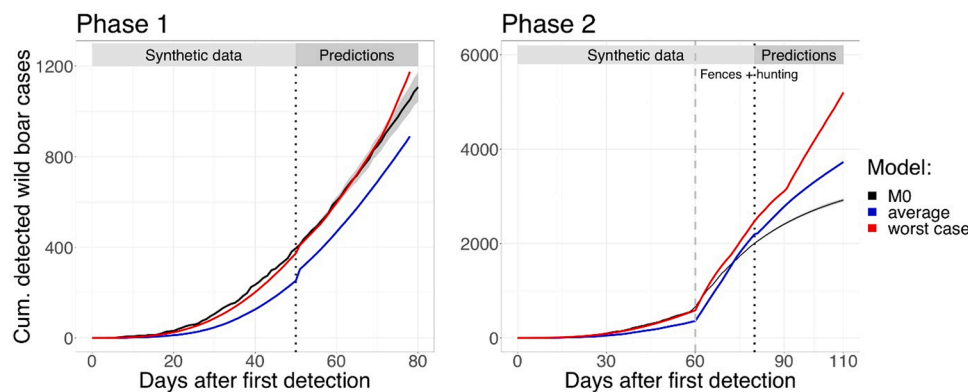


Fig. 3. Predicted cumulative numbers of detected wild boar cases according to two ensemble models (average and worst-case) compared to model M0 trajectories, between days 50 and 80 ("Phase 1"), and between days 80 and 110 ("Phase 2"), including the four team models providing dynamic predictions (CIRAD, INRAE, Massey, UK). The dotted line delimits the prediction period for each phase of the challenge. The dashed line shows when fences were implemented and intensive hunting started. Projections assumed similar control measures during the prediction period and the observed period. Model M0 was used to produce synthetic data up to the beginning of the prediction period (using the stochastic repeat selected for the challenge), then 500 stochastic repetitions were simulated to show possible variability over the prediction period (very low during Phase 2).

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these phases.

3.3.1. Spatial distribution of detected pig farm cases

Fig. 4 provides the spatial predictions, i.e., the probabilities of ASF being detected on farms over the prediction period. Only the CIRAD team successfully predicted the detection of an infected farm far away from the primary case (Fig. 4A), despite the use of a non-stochastic approach. Other teams were better at predicting detection of infected farms in the vicinity of the primary case. In addition, a relatively low probability cut-off value should be used for the detection index to be high enough (Fig. 5). The Massey and UK teams had more sensitive spatial predictions when we assessed the ability of models to predict the exact location of future outbreaks (Fig. 5A). Such models could help prioritise areas to survey, instead of relying only on back-tracing to identify at-risk contacts. Models were much better at predicting approximate outbreak locations (i.e., identifying hotspots), as indicated by the greater sensitivity of predictions made by most teams under this scenario (Fig. 5B). Specificity of teams' model predictions was high (>99% for a cut-off > 0.03), due to the huge number of uninfected pig farms, thus was not shown.

We also explored spatial predictions through ensemble models (Fig. 6) and assessed the associated detection index (Fig. 7). Average and weighted average ensemble models were less sensitive than the UK and Massey models, especially for high cut-off values. In contrast, the worst-case and the threshold-average ensemble models had a better detection index than all team-models, even for predicting the exact locations of future cases.

3.3.2. Spatial distribution of detected wild boar infections

Three teams (INRAE, CIRAD, Massey) provided spatial predictions for the number of infected wild boar detected in a spatial location for phase 2 (days 80–110; Fig. 8). Those simulations were used to calculate the probability of detecting infected wild boar in specific tiles (hexagons in the INRAE and CIRAD models vs. squares in the Massey model). The INRAE model was the most sensitive here, probably due to the larger tile size. However, the INRAE model predicted the occurrence of a second cluster in the south-west of the area with a probability of 0.5 (Fig. 8). Such a cluster did not occur in the selected synthetic data produced by model M0. Teams' models agreed that the virus had a high probability of escaping from the fenced zone by its south-west corner.

Despite the low number of models included, we compared the results of ensemble models to the selected trajectory in model M0 (Fig. 9). All ensemble models were largely influenced by INRAE predictions. As a result, the shape of the first predicted cluster in the worst-case model looked similar to INRAE predictions, and a second cluster was also predicted, but with a lower probability in the average model than in the individual INRAE model. By definition, the worst-case model was the most sensitive. However, the threshold-average ensemble models were as sensitive as the worst-case and the INRAE models, even for the highest tested probability threshold (Fig. 10).

3.4. Effectiveness of alternative control measures

Table 2 summarises the control measures modelled by all teams during the challenge. Choices made in phase 1 sometimes limited a team's ability to test measures in phase 2. Some teams thus had to choose between adapting their models to make the requested

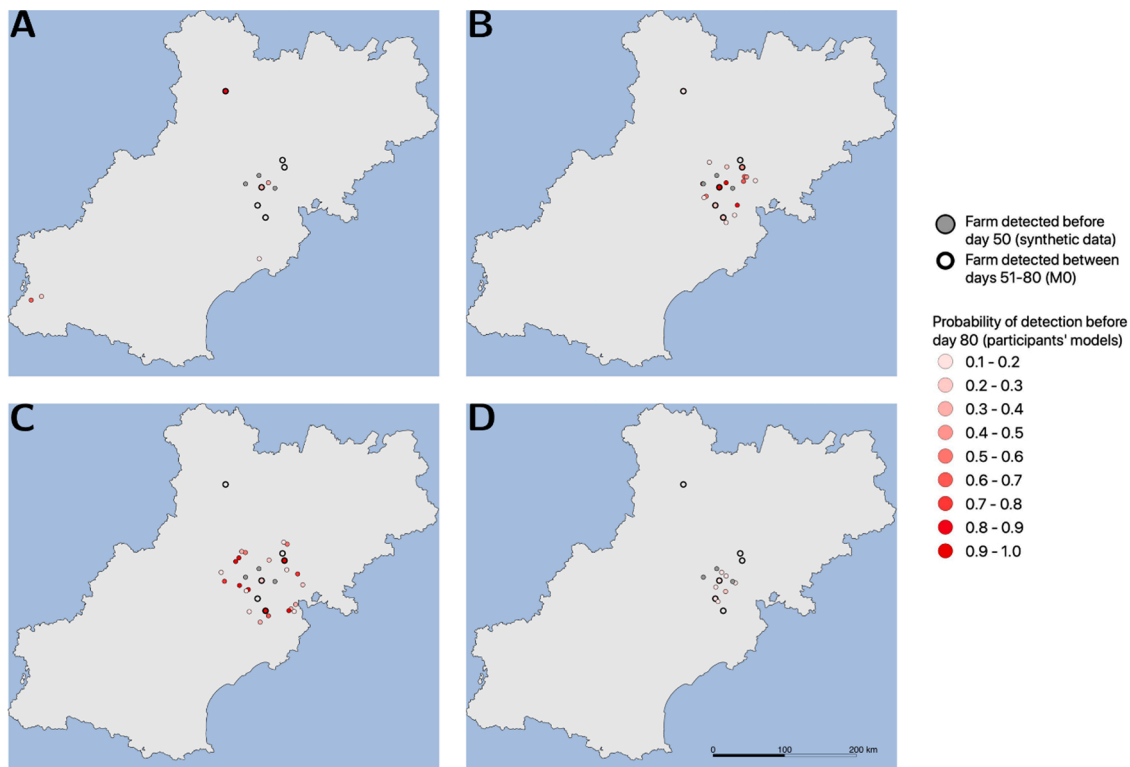


Fig. 4. Probability of detecting ASF outbreaks on pig farms between days 50 and 80 without additional control measures, as calculated by each team. Black circles indicate farms that would have been detected in model M0 with the selected trajectory in the absence of additional control measures. Teams that provided spatial predictions for phase 1 were: CIRAD (A); UK (B); Massey (C); WUR (D).

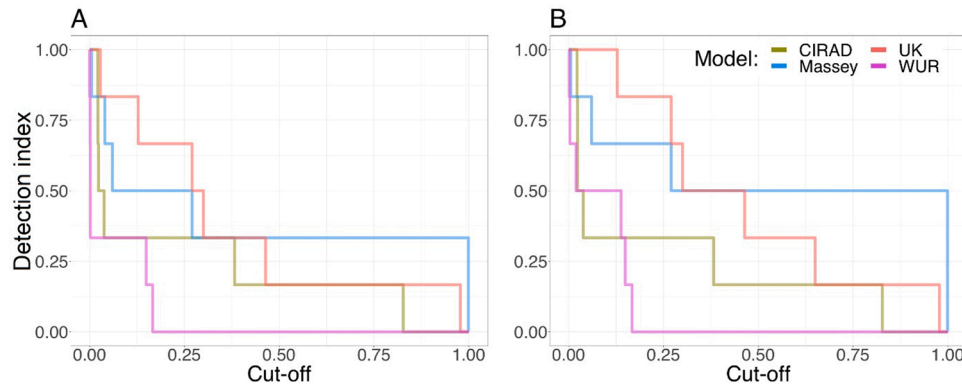


Fig. 5. Detection indexes of teams' model predictions regarding the location of detected infected pig farms between days 50 and 80, without additional control measures. The detection index D_k for team k was calculated as the proportion of pig farms (among a total of N_{PF} farms) predicted to be detected as infected with a probability above the cut-off value (x-axis), given that they were truly detected as infected in the selected synthetic data. A: based on exact locations of pig farm outbreaks. B: with a 15-km tolerance on the locations of pig farm outbreaks, i.e., predictions of detected ASF infections on pig farms were classified as correct if those farms were located within 15 km from a farm that was detected as infected in the selected synthetic data.

calculations, or not testing all the proposed measures. In addition, teams did not interpret control measures in comparable ways, which limits comparisons. Heterogeneity in control measure implementation and the format of model outputs did not allow quantitative comparisons, in most cases, thus teams' findings were compared qualitatively.

In phase 1, the control measures concerned only wild boar. Tested measures showed no effect on pig farms, except the CIRAD team who showed that (if effective) fences could limit virus spread to the east and north of the island, thus pig farms in those areas would receive a degree of protection by not being in direct contact with infected wild boar. In line with results from model M0, the teams agreed that fences alone had no significant effect on the total number of detections of infected wild boar within the prediction period. When hunting pressure was increased in model M0, the number of detections by carcass discovery over the prediction period decreased by 50%, while the number of detections by hunting increased by 1660%. The Massey team quantified the latter at

almost 1000%, while the INRAE team estimated it at 120%. The INRAE team did not include the increased test rate among hunted wild boar, which explains the discrepancy. The outputs of the other teams did not allow for such an assessment. Here, the number of detected cases is not a relevant marker of effectiveness of control measures - reducing the total number of cases (detected and not detected) is the actual objective of control strategies. Spatio-temporal discontinuities in the intensity of both active searches and hunting lead to temporal changes in the detection rate, thus the total number of detected cases does not provide a reliable proxy for the total number of cases. Only the INRAE team quantified the variation in the total number of cases, predicting a reduction in cases in the intensive hunting scenario. Despite underestimating the absolute number of cases (1100 vs. 2500 with model M0), the relative reduction in cases over the prediction period proved to be fair (both predicting a decrease of 13%). The INRAE model predicted a similar effectiveness of fences with and without intensive hunting,

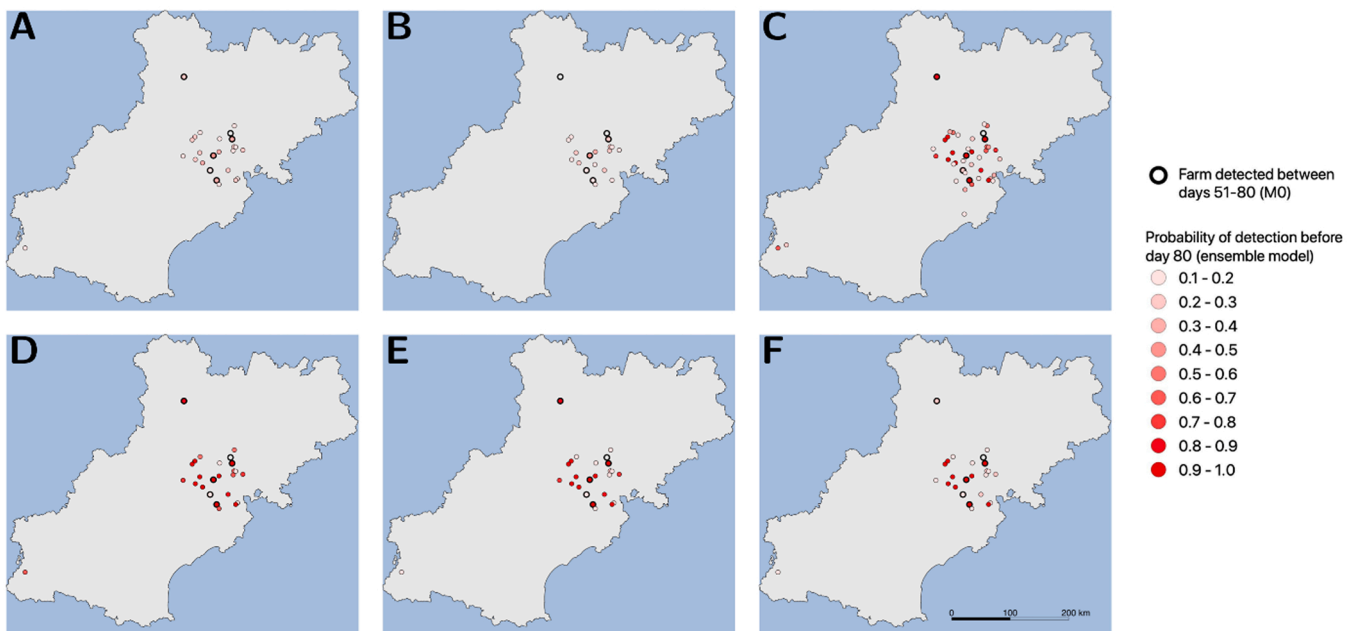


Fig. 6. Probability of detecting ASF outbreaks on pig farms between days 50 and 80 without additional control measures, as calculated with ensemble models based on the four available team models for this output. Black circles indicate farms that would have been detected in model M0 with the selected trajectory in the absence of additional control measures. The ensemble models shown are: average (A); weighted average (B); worst-case (C); and threshold-average with threshold values of 0.5 (D), 0.7 (E) and 0.9 (F).

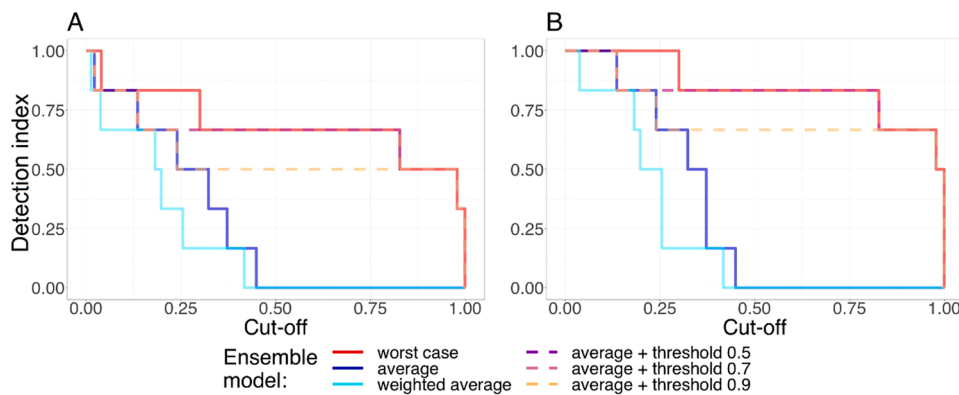


Fig. 7. Detection indexes of ensemble model predictions regarding the location of detected infected pig farms between days 50 and 80, with no additional control measures during the prediction period. A: based on exact locations of pig farm outbreaks. B: with a 15-km tolerance on the locations of pig farm outbreaks, i.e., predictions of detected ASF infections on pig farms were classified as correct if those farms were located within 15 km from a farm that was detected as infected in the selected synthetic data.

whereas a scenario with fences but no intensive hunting was inefficient with model M0. The impact of the measures on the spatial distribution of cases in wild boar can be seen visually on the incidence maps provided by teams and the detection probability maps produced by the ensemble models. In phase 1, with model M0, fences with or without intensive hunting did not trigger a change in the distribution area of detected wild boar cases. The Massey and the INRAE teams reached the same conclusion. The CIRAD team only tested the implementation of fences and concluded that, given its location, the fence could not completely contain the epidemic, since ASF was already spreading to the south-west of the fence. The CIRAD team predicted that fences could have been effective had they been implemented seven days earlier and if very few wild boar escaped through the fences. Only the UK team predicted a reduction in the area detected as infected when fences were in place with intensive hunting from day 60.

In phase 2, most of the measures concerned pig farms, except the extension of the area for active search around detected infected wild boar carcasses, which increased the capacity to detect infected wild boar (Fig. 11). All teams (including Massey and INRAE teams that modelled transmission from pig farms to wild boar) concluded that the alternative

control measures in pig farms had little or no effect on the spread of the epidemic among wild boar compared to the baseline scenario, with relative differences in detected cases of at most about 10% (Fig. 11A). The measures had a slightly stronger effect on the number of detected infected pig farms, although results were heterogeneous between teams (Fig. 11B). The measures that reduced the number of detected cases in pig farms by more than 25% in model M0 were: (1) the elimination of pig farms located near a detected wild boar infected carcass (effect found by the CIRAD and UK teams), and (2) the elimination of pig farms located in the protection zone (effect found by INRAE). However, as the number of infected pig farms was small, the absolute difference in detected cases remained small. Furthermore, the number of exposed but uninfected farms that would have been culled if this measure had been implemented was not explicitly requested and thus was not provided by the teams, but was likely to be high and should be taken into account when evaluating such a measure. Finally, all teams concluded that the alternative measures did not have a sufficient effect - particularly among wild boar - and to justify their implementation.

In phase 3, the teams were asked to predict how likely it was that the

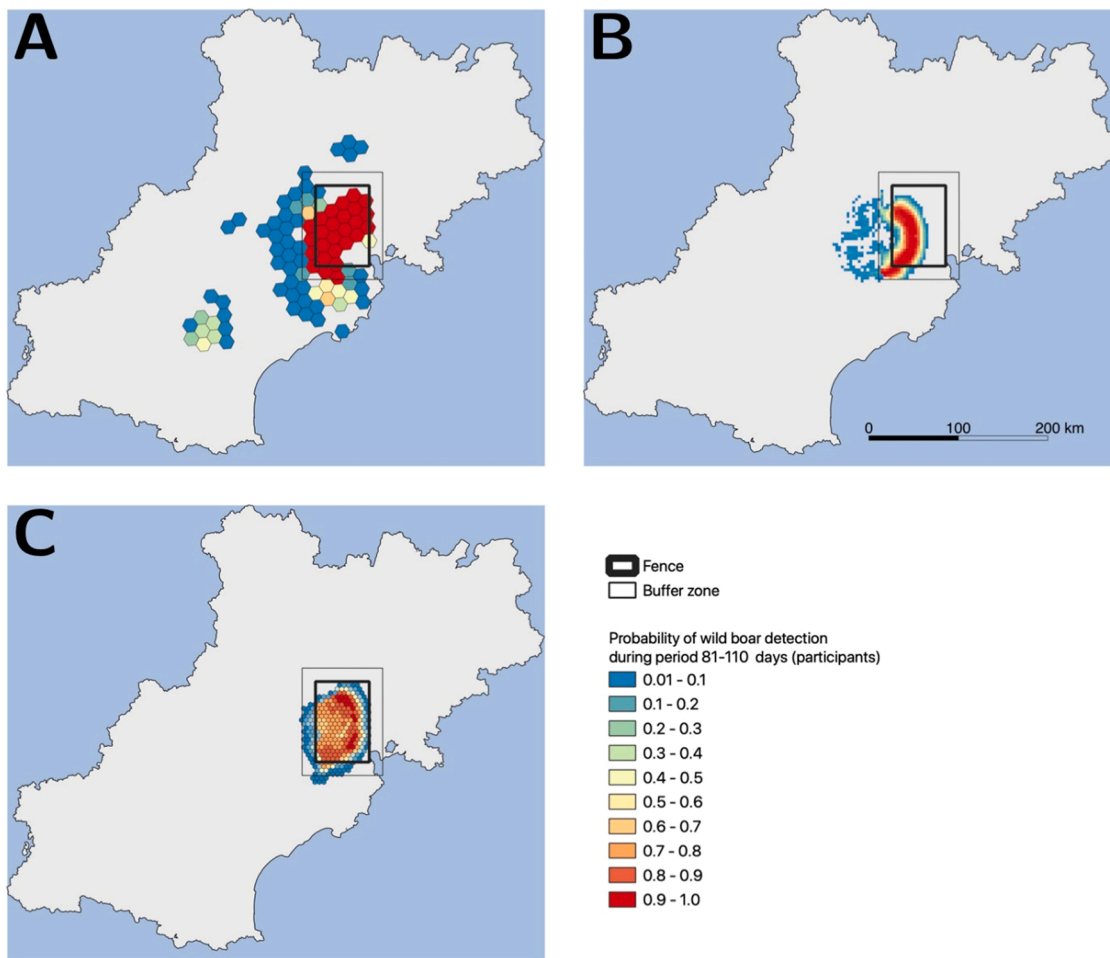


Fig. 8. Predicted probability of detecting infected wild boar between days 80 and 110, without additional control measures after day 80, as calculated by three teams that provided spatial predictions for phase 2: INRAE (A, 195 km² tiles), Massey (B, 1 km² tiles), CIRAD (C, 86.6 km² tiles).

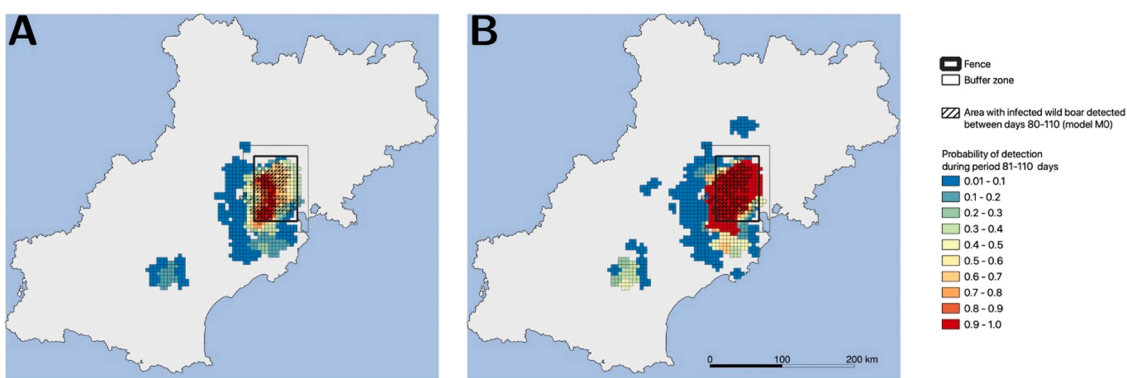


Fig. 9. Predicted probability of detecting infected wild boar between days 80 and 110 without additional control measures after day 80, calculated with ensemble models on 5 × 5 km² tiles. Marked tiles: tiles where infected wild boar were detected in model M0 with the selected trajectory made in the absence of additional control measures after day 80. A: average, B: worst-case.

epidemic would fade out over the following four months if intensive hunting ceased at day 110. Only the INRAE team considered it could be stopped, while other teams advised to continue this measure. This was in line with model M0's predictions, which showed a high number of infected wild boar carcasses despite a very low number of detected wild boar cases 230 days after the first detection, thus indicating a low probability of extinction (Picault et al., 2022). The CIRAD team advised that the buffer zone should be extended to prevent spread towards the

south-west.

3.5. Participants' feedback

Eleven participants out of 46 from 10 teams (including those that did not finish the challenge) provided feedback on the organisation of the ASF Challenge. Overall, respondents found that it was extremely useful to receive test data before the start of the challenge and that the data

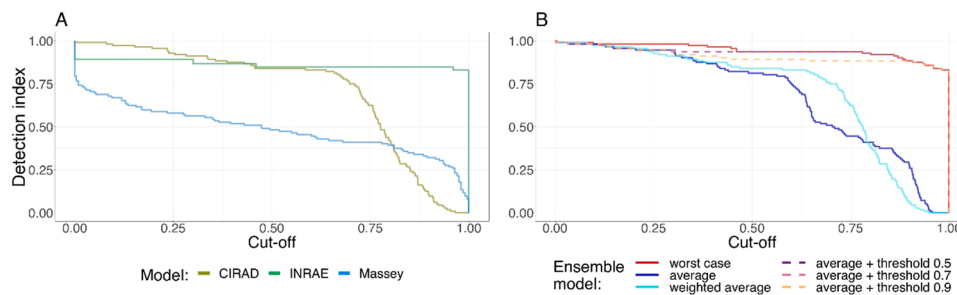


Fig. 10. Detection indexes of predictions, from teams' models (A) and ensemble models (B), regarding the probability of detecting wild boar cases within $5 \times 5 \text{ km}^2$ tiles between days 80 and 110, assuming that no additional control measures were introduced after day 80.

Table 2

Alternative control measures modelled by teams. Control measures imposed by ASF regulation were accounted for in all models. No alternative measure was tested in phase 3.

Control measures ^a	CIRAD	UK	INRAE	Massey	WUR
Phase 1					
Fences	x ^b	x	x	x	
Fences + intensive hunting		x	x	x	
Phase 2					
Fences + intensive hunting (included in baseline)	x	x	x	x	x
Culling on pig farms (PF) in protection zone	x	x	x	x	x
Culling on traced PF	x	x	x	x	
Culling on PF located $\leq 3 \text{ km}$ from detected WB cases	x	x		x	x
Extend surveillance zone radius from 10 to 15 km		x	x	x	
Extend radius of active search around detected WB cases from 1 to 2 km	x		x	x	

^a Protection zone has a radius of 3 km around detected PF; traced PF have exchanged animals with a detected PF in the 3 weeks before detection.

^b Various dates and fence efficacy values were tested.

format and the documentation provided were appropriate and relevant. Respondents were less consensual on the calendar of the challenge. Indeed, some raised the issue that keeping pace with all other activities running at the same time, especially when some team forces were parallelly devoted to COVID-19 pandemic modelling, was difficult. Indeed, the ASF Challenge was a voluntary exercise and not a real-time problem-solving exercise during a health crisis when all efforts would have been devoted to providing policy recommendations. All teams had strong expertise in mechanistic modelling and programming. Some teams reported that they lacked some prior understanding of ASF epidemiology

and expertise in wild boar ecology. Eight and nine participants considered that the ASF Challenge improved their modelling skills and their ability to provide real-time support to policy-making, respectively. It was also highlighted that the ASF Challenge was useful to improve team management skills and enhance remote collaborations in a timely fashion. Nine respondents indicated they would be interested in participating in another modelling challenge, either on ASF or another infectious disease of livestock such as avian influenza. Ten of the eleven respondents indicated they would recommend to other colleagues to participate in such modelling challenges. Expectedly, it was regularly highlighted that the COVID-19 pandemic and associated restrictions limited the opportunity to meet other people in the field of infectious disease modelling, which was one of the main objectives of the ASF Challenge.

4. Discussion

4.1. Key results and novelty

The ASF Challenge was the first modelling challenge in animal epidemiology. During this challenge, five international research teams developed models predicting the evolution of ASF over six months following its emergence in an isolated territory. This epidemic dynamic was simulated by the organising team and was therefore entirely fictitious, even though the model used was calibrated with plausible parameter values and informed by expert knowledge (Picault et al., 2022).

The study of a multi-species disease allowed us to address the problem of integrating the interface between two interacting and dynamic biological components in an epidemiological model. To effectively integrate this interface, teams mainly developed stochastic mechanistic compartmental models. On one hand, stochastic frameworks could be preferred because at epidemic onset, the effect of chance is high (small number effects), and because of the occurrence of rare

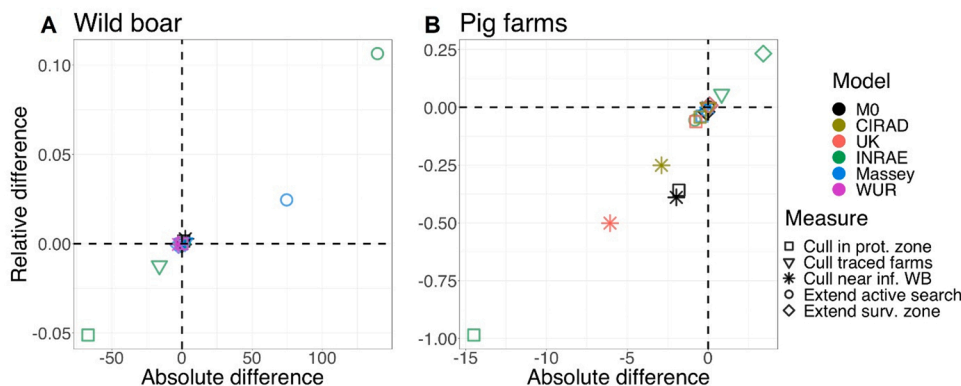


Fig. 11. Effectiveness of alternative control measures in phase 2. Five measures were tested: the culling of pigs in farms located in the protection zone (square); the culling of pigs in farms traced as having had contact with a detected farm (inverted triangle); the culling of pigs in farms located in the vicinity of a detected infected wild boar (star); the extension of the active search zone around detected infected wild boar carcasses (circle); and the extension of the surveillance zone (rhombus). For each control measure, and for each model, effectiveness was calculated as the absolute and relative differences in the number of detected wild boar cases (A) and detected pig farm outbreaks (B) during the prediction period between simulations with and without the control measure.

events in a complex biological system involving multiple interacting host species (e.g., long distance ASF dispersion, indirect infectious contact between farms, infectious contact between livestock and wildlife). On the other hand, compartmental models provide a relevant balance between parsimony (not only individual-based processes) and accuracy (accounting for within-population dynamics when necessary). Originally, a probabilistic model for pig farms was used by one team. Although that model was not integrated with a dynamic simulation model, it still displayed a good predictive ability. No black-box models (e.g., based on machine learning) were used. Overall, the explicit modelling of epidemiological events, particularly at the interface between wild and domestic fauna, was deemed necessary by the researchers to accurately predict the epidemiological extent of the disease and to test the control measures requested by the organisers.

The course of the epidemic was in general predicted well by the teams. The temporal predictive ability was better for domestic animals than for wildlife. During the course of the ASF Challenge, the predictions of the situation on farms, although already good during phase 1, improved with each successive phase, thanks to the modellers' hindsight and the increased quantity of available data. In contrast, several factors – including uncertainty regarding host distribution, the implementation of fences, intensive hunting, the greater number of hidden compartments and a lower detection probability – made the modelling of the wildlife situation more complex and thus limited the predictability of ASF dynamics among wild boar. The same conclusions applied to the spatial performance of the models, which were evaluated for the first time in the context of an epidemiological challenge. Small spatial units were considered necessary by most of the teams in order to assess local management strategies for a virus that essentially spreads in wildlife via proximity contacts. An interesting result was that, despite heterogeneity among teams in the predicted temporal trajectories of wild boar cases, there was relative homogeneity in the predicted temporal trajectories of pig farm cases. This paradoxical result suggests that the methods used to model risk in pig farms were relatively insensitive to systematic biases within the wild boar models. This is reassuring from a risk management point of view, given that there are typically large uncertainties regarding the density, distribution, and dynamics of sylvatic reservoir host populations.

No single model developed by any one team was better than all other models on every aspect of the challenge, confirming the value of considering multiple approaches when advising policy makers, as was also highlighted for controlling foot-and-mouth disease in a multi-model framework (Probert et al., 2016; Webb et al., 2017). Multiple model approaches can add weight to conclusions when models are in agreement, overcoming limits to inferential power that arise when there are large uncertainties in the predictions of a single model. Indeed, ensemble models can be constructed, by integrating the predictions of all models, allowing the complementary predictions of each model to be exploited. The temporal ensemble models showed very good predictive ability. To the best of our knowledge, this is the first time that small-scale spatio-temporal ensemble models have been developed during a challenge. For this, homogenisation of spatial units was performed, followed by aggregation of the results from different teams. One limit of the proposed ensemble models was not to account explicitly for teams' prediction uncertainty. Since teams did not provide similar numbers of repetitions (ranged from one to 10,000 repetitions, depending on challenge phase and team) it was difficult to integrate output variability in the ensemble models. We thus chose to build several simpler ensemble models (teams' average; weighting average with weights proportional to the number of repetitions; choosing worse-case predictions). Another approach would have been to require a minimum number of repetitions per output per team to facilitate the calculation of prediction intervals, or to have a sufficient number of teams involved in the challenge to assess confidence interval of ensemble models (which was not relevant here as we included only a few models).

4.2. Main issues encountered during the ASF Challenge

Incomplete knowledge regarding the wildlife component, especially the population size and ecology of wild boar (Giménez-Anaya et al., 2020), presented a key difficulty for both the teams and the organisers of the ASF Challenge. Knowledge on livestock is typically much more complete than data related to wildlife, even more so than for human populations in many respects. Indeed, legislation governing the declaration of farm animals in Europe provides detailed knowledge of their distribution and movements (Brooks-Pollock et al., 2015). This, in combination with greater detection probabilities and lower uncertainties, can help explain the greater predictive performance of teams' models for the domestic part as opposed to the sylvatic part of the biological system. This situation illustrates a difficulty faced by modellers when confronted with real-life emergence or re-emergence of infectious diseases in wildlife, and emphasises the need to improve wildlife disease surveillance and wildlife population monitoring to improve preparedness (Cardoso et al., 2022).

The freedom given to teams allowed the development of several models with different assumptions and scales, as well as the genesis of a few new ideas for control measures. This freedom helped foster diversity in modellers' choices regarding how to characterise the spatial or temporal aspects of the epidemic in order to answer the posed management questions. In contrast, it was not possible to assess in this challenge the specific role of the spatial unit as only one unit was implemented for each method. Team models differ by many other confounding factors. Thus, performance indicators cannot be defined as a function of the spatial unit size. The choice of the spatial unit could have important impacts in guiding decision making. Evaluating the effect of the spatial resolution of epidemiological models on their performance is thus an interesting perspective for future modelling challenges.

The freedom given to teams also led to heterogeneity in the type and format of model outputs, which made it difficult to compare models and their predictions. Teams provided results using various forms of temporal and spatial aggregation, often without providing output from all epidemiological compartments needed for comparison. They chose which outputs to provide among all those generated by their respective models: some favoured infection events (the UK and INRAE teams), others the distribution of some sub-set of epidemiological states (the CIRAD and Massey teams), and some limited the provided model output to the quantities strictly needed for answering the questions, i.e., detected infections (the WUR team). Finally, some teams provided model code. Although open source code is important for transparency and reproducibility and allows opportunities for interaction with external examiners, in practice it is an inferior substitute for standardised format prediction data files. Particularly during a real health crisis, health managers would not have the time to read, understand, and re-run each model code, nor to communicate extensively with modelling teams.

The suite of different models allowed the evaluation, by at least three different teams (see Table 2), of the effectiveness of each of the control measures envisaged by the organisers. The links made between wildlife and livestock conditioned the evaluation of some control measures. To simulate these measures, teams adapted their models, especially the details of spatial representation, but without modifying their basic modelling frameworks, because of time constraints. The implementation of intensive hunting, a key management measure of ASF, was one of the most problematic issues for both teams and organisers. For example, the effects of an intensive hunting campaign on wild boar ecology and movement patterns were not taken into account in model M0, because they remain largely unknown. Indeed, intensive hunting could increase the home range (Lange, 2015) and contacts between wild boar, and also induce stress-related immunosuppression, and therefore risk intensifying viral transmission (Miguel et al., 2020). Such effects of hunting have been reported for badgers in the case of bovine tuberculosis control (Donnelly et al., 2003; Riordan et al., 2011; Woodroffe et al., 2006).

4.3. Lessons learned

The complementarity of several proposed approaches is interesting in the case of a real health crisis. Indeed, ensemble models of the temporal and spatial dynamics of an epidemic take advantage of all the predictions made by the different approaches within a framework that allows a great level of freedom. In our framework, they did not always achieve better predictive ability than all teams' models, contrary to what was achieved in past challenges (Johansson et al., 2019; McGowan et al., 2019; Viboud et al., 2018). One explanation is the low number of models integrated in the ensemble models. In particular, heterogeneity in the format of outputs sent by teams only allowed for three models to be integrated into the spatial ensemble models for wildlife. Moreover, the proposed models were not extremely different in essence. In future challenges, or real outbreaks, giving teams greater and earlier guidance regarding the required format of submitted model outputs could greatly facilitate the building of ensemble models. Despite these limitations, the methodology for building these ensemble models with high spatial resolution was developed for the first time in a challenge, which represents a major step forward. This is certainly an avenue to be pursued to further improve the predictive ability of epidemiological models. Nevertheless, we noted that, if one of the individual models already provided accurate predictions of a given output, incorporating less accurate predictions from another model into an ensemble model resulted in signal degradation. During a real health crisis, to minimise this risk, when building ensemble models higher weight could be given to team models that had outperformed other models over the previous prediction period once observations were available to assess the models' predictive abilities. One option would be to weight a model proportionally to the likelihood of observations given that model's predictions in the previous phase. Such a weighting should nevertheless be implemented with caution, because top-performing models may differ during the course of an epidemic, as was observed in this challenge. During future challenges, and in contrast to what has been done so far in existing challenges, organisers could also consider making this step an open-source endeavour, through a shared platform, to facilitate cooperation, task sharing, communication, and homogenisation of formats.

If the aim of a challenge is to rank the performance of the different models and establish ensemble models, a stricter framework should be favoured. This was achieved in the seasonal influenza (Biggerstaff et al., 2016; Reich et al., 2019) and dengue (Johansson et al., 2019) challenges, where teams had to provide probability distributions over pre-defined intervals of strictly defined outputs. It was also the case in the consortium built to assess control measures of foot-and-mouth disease in a multi-model framework, using existing models in a collaborative way (Webb et al., 2017). More evaluation tools are then applicable to analyse team outputs (Gneiting and Raftery, 2007). Organisers thus should be aware of possible limitations that can arise when lots of freedom is granted to teams, and balance the flexibility that this freedom offers against the time required to collate and analyse all teams' outputs. An alternative option would be to make greater use of individual strengths and experience within teams by enabling the collaborative analysis of teams' results. The added dynamism of such a collaboration would be particularly useful during a real outbreak.

The objective of the challenge was not to generate recommendations for ASF control but rather to improve our preparedness. However, stakeholders could have been engaged more in the challenge, to advise on when and how models could be useful, and also to improve communication between scientists and disease managers. During a real health crisis, science-based models need to support timely policy and decision making. Thus, decision makers need to be consulted on choices about the level of freedom granted to modelling teams, whilst recognising that independent modelling teams may take completely different complementary approaches, which can reveal different aspects of the epidemics. Clarity of communication with modellers is key, in both directions, as communication issues can lead to a misunderstanding of the

control measures to be tested, and thus inappropriate representation within models, possibly altering conclusions, as has sometimes been the case during this challenge (where the organisers played the role of decision makers). The provision of clear metadata by the teams during the challenge also seems to be a required improvement, especially if some freedom is given to the teams. This would improve the comparability of outputs and figures provided by the teams. Communication issues, already lamented elsewhere (Metcalfe et al., 2015; Webb et al., 2017), are crucial, and particular vigilance is required on behalf of modellers and public animal health managers. In addition, despite time constraints, most teams also tested for additional scenarios not defined in the challenge, highlighting that modellers could be a driving force behind innovative proposals during epidemics. Also, in phase 3, teams were asked to advise about other alternative measures that could be considered (without testing them with their model), which resulted both in proposals to modify existing measures (e.g., build new fences, enlarge the buffer zone around fences) or to new ideas (e.g., restrictions in movement distances, sequestration of domestic pigs).

In our study, the epidemic was fictitious, as was the case during the Ebola challenge (Viboud et al., 2018). An important advantage of using synthetic data is providing complete control and knowledge of the epidemiological situation, mechanisms and parameters, whilst maintaining a realistic course of the epidemiological dynamics (Ajelli et al., 2018). It enables the control of noise within the data. It also enables the assessment of control measures for which decision makers seek advice, in addition to the implemented control measures. The synthetic aspect of the challenge was appreciated by participating teams, as it allowed a complete exercise in a non-emergency animal-health context. The omniscience obtained by the synthetic aspect of the epidemic allowed for many additional comparisons that would not be possible during a real crisis. Thus, while the analysis focused mainly on predictions of the observed situation (via case detections) to mimic a real situation, it could be complemented by the analysis of total cases (including undetected cases, e.g., to assess interventions) when such information is provided by the participants. This approach was not taken in previous challenges, nor was it taken here, since most teams chosen not to record total cases in order to economise computational resources. Moreover, total infections can be more difficult to predict than case detections, especially when detection effectiveness is imperfect and heterogeneous in space or time, as was the case for wild boar in this challenge. This should be an important consideration in future modelling challenges based on synthetic epidemics. Finally, a mechanism that has not been accounted for to date, that would clearly be interesting for future challenges, are the evolutionary dynamics of pathogens and the important impacts that they can have on epidemics. The importance of pathogen evolution has been highlighted all too clearly in the recent COVID 19 crisis with SARS-CoV-2 (Dyson et al., 2021; Koopman et al., 2021). However, teams would need genetic sequence data, in which case using data from a real epidemic may be a more convenient option than using synthetic data.

The model built to generate the synthetic data utilised current knowledge of ASF (Korennoy et al., 2014; Nigsch et al., 2013; Vergne et al., 2016) and interactions with ASF experts helped us define model assumptions. However, model predictions have not been compared with real historical disease data. This would have enabled an assessment of the model's ability to predict the evolution of a real epidemic as was done during the Ebola challenge (Viboud et al., 2018). Another aspect that could be improved, when relying on synthetic data, is to consider different epidemic trajectories (repetitions of model MO) as alternative sets of observed data. Indeed, using a trajectory close to the mean/-median of the generative process or a more "atypical" trajectory having, a priori, a lower probability of occurring, could lead to different results by the different models of the challenge.

In the current challenge, there was no need for immediate real-time analysis and comparison of team-results, since this was not a real animal health crisis. The comparative analyses were therefore all carried out

after the completion of the challenge. In addition to the lack of feedback to the teams, this also limited the early identification of problems in understanding the exact definition of the measures, as well as the anticipation of problems arising from the reporting of aggregated data by the teams. Future challenges will have much to gain from analysing results during the course of the challenge. If, as here, the challenge is based on synthetic data, our experience shows that providing test data to teams prior to the challenge allows teams to anticipate the format of their inputs. Extending this to include example predictions, if teams are expected to provide homogenised outputs, would greatly facilitate comparison and the building of ensemble models.

Open international challenges in epidemiology are time-consuming and require a significant involvement of organising and participating teams. Yet, they demonstrate a great potential, because they contribute to improving the preparation of the scientific community for future infectious disease emergence events. In particular, the study of infectious diseases emerging at the interface between wildlife and humans seems necessary in view of the increasing frequency of their occurrence (Bengis et al., 2004) and the dramatic consequences they may have.

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CRediT authorship contribution statement

Pauline Ezanno: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft. **Sébastien Picault:** Conceptualization, Formal analysis, Investigation, Methodology, Software, Supervision, Validation, Visualization, Writing – original draft. **Servane Bareille:** Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – review & editing. **Gaël Beaunée:** Data curation, Methodology, Investigation, Visualization, Validation, Writing – review & editing. **Gert Jan Boender:** Data curation, Methodology, Investigation, Visualization, Validation, Writing – review & editing. **François Deslandes:** Data curation, Methodology, Investigation, Visualization, Validation, Writing – review & editing. **Thomas J. Hagenaars:** Data curation, Methodology, Investigation, Visualization, Validation, Writing – review & editing. **Ferran Jori:** Data curation, Methodology, Investigation, Visualization, Validation, Writing – review & editing. **Matthieu Mancini:** Data curation, Methodology, Investigation, Visualization, Validation, Writing – review & editing. **David R.J. Pleydell:** Data curation, Methodology, Investigation, Visualization, Validation, Writing – review & editing. **Elisabeta Vergu:** Data curation, Methodology, Investigation, Visualization, Validation, Writing – review & editing. **Matthieu Vignes:** Data curation, Methodology, Investigation, Visualization, Validation, Writing – review & editing. **Timothée Vergne:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Supervision, Validation, Visualization, Writing – original draft.

Declaration of interest

The authors have no conflict of interest.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.epidem.2022.100615](https://doi.org/10.1016/j.epidem.2022.100615).

References

- Ajelli, M., Zhang, Q., Sun, K., Merler, S., Fumanelli, L., Chowell, G., Simonsen, L., Viboud, C., Vespignani, A., 2018. The RAPIDD Ebola forecasting challenge: model description and synthetic data generation. *Epidemics* 22, 3–12. <https://doi.org/10.1016/j.epidem.2017.09.001>.
- Andronico, A., Courcoul, A., Bronner, A., Scoizec, A., Lebouquin-Leneveu, S., Guinat, C., Paul, M.C., Durand, B., Cauchemez, S., 2019. Highly pathogenic avian influenza H5N8 in south-west France 2016–2017: a modeling study of control strategies. *Epidemics* 28, 100340. <https://doi.org/10.1016/j.epidem.2019.03.006>.
- Bengis, R.G., Leighton, F.A., Fischer, J.R., Artois, M., Mörmr, T., Tate, C.M., 2004. The role of wildlife in emerging and re-emerging zoonoses. *OIE Rev. Sci. Tech.* 23, 497–511. <https://doi.org/10.20506/rst.23.2.1498>.
- Benincà, E., Hagenaars, T., Boender, G.J., van de Kastele, J., van Boven, M., 2020. Trade-off between local transmission and long-range dispersal drives infectious disease outbreak size in spatially structured populations. *PLoS Comput. Biol.* 16 (7), e1008009. <https://doi.org/10.1371/journal.pcbi.1008009>.
- Biggerstaff, M., Alper, D., Dredze, M., Fox, S., Fung, I.C.H., Hickmann, K.S., Lewis, B., Rosenfeld, R., Shaman, J., Tsou, M.H., Velardi, P., Vespignani, A., Finelli, L., for the Influenza Forecasting Contest Working Group, 2016. Results from the centers for disease control and prevention's predict the 2013–2014 Influenza Season challenge. *BMC Infect. Dis.* 16, 357–367. <https://doi.org/10.1186/s12879-016-1669-x>.
- Boender, G.J., van den Hengel, R., van Roermund, H.J.W., Hagenaars, T.J., 2014. The influence of between-farm distance and farm size on the spread of classical swine fever during the 1997–1998 epidemic in the Netherlands. *PLoS ONE* 9 (4), e95278. <https://doi.org/10.1371/journal.pone.0095278>.
- Brooks-Pollock, E., de Jong, M.C.M., Keeling, M.J., Klinkenberg, D., Wood, J.L.N., 2015. Eight challenges in modelling infectious livestock diseases. *Epidemics* 10, 1–5. <https://doi.org/10.1016/j.epidem.2014.08.005>.
- Cardoso, B., Garcia-Bocanegra, I., Acevedo, P., Caceres, G., Alves, P.C., Gortazar, C., 2022. Stepping up from wildlife disease surveillance to integrated wildlife monitoring in Europe. *Res. Vet. Sci.* 144, 149–156. <https://doi.org/10.1016/j.rvsc.2021.11.003>.
- Dankwa E.A., Lambert S., Hayes S., Donnelly C.A., Thompson R.N., sub. 2022. Stochastic modelling of African swine fever in wild boar and domestic pigs: epidemic forecasting and comparison of disease management strategies. Submitted to the special issue ASF Modelling Challenge of Epidemics.
- Beaunée, G., Deslandes, F., Vergu, E., sub. 2022. Inferring A.S.F. transmission in domestic pigs and wild boars using a paired model iterative approach. Submitted to the special issue ASF Modelling Challenge of Epidemics.
- Del Valle, S.Y., McMahon, B.H., Asher, J., Hatchett, R., Lega, J.C., Brown, H.E., Leany, M. E., Pantazis, Y., Roberts, D.J., Moore, S., Peterson, A.T., Escobar, L.E., Qiao, H., Hengartner, N.W., Mukundan, H., 2018. Summary results of the 2014–2015 DARPA Chikungunya challenge. *BMC Infect. Dis.* 18, 245. <https://doi.org/10.1186/s12879-018-3124-7>.
- Dixon, L.K., Stahl, K., Jori, F., Vial, L., Pfeiffer, D.U., 2020. African swine fever epidemiology and control. *Annu. Rev. Anim. Biosci.* 8, 221–246. <https://doi.org/10.1146/annurev-animal-021419-083741>.
- Donnelly, C.A., Woodroffe, R., Cox, D.R., Bourne, J., Gettinby, G., Le Febvre, A.M., McInerney, J.P., Morrison, W.I., 2003. Impact of localized badger culling on tuberculosis incidence in British cattle. *Nature* 426 (6968), 834–837. <https://doi.org/10.1038/nature02192>.
- Dyson, L., Hill, E.M., Moore, S., Curran-Sebastian, J., Tildesley, M.J., Lythgoe, K.A.A., House, T., Pellis, L., Keeling, M., 2021. Possible future waves of SARS-CoV-2 infection generated by variants of concern with a range of characteristics. *Nat. Commun.* 12, 5730. <https://doi.org/10.1038/s41467-021-25915-7>.
- Ezanno, P., Andraud, M., Beaunée, G., Hoch, T., Krebs, S., Rault, A., Touzeau, S., Vergu, E., Widgren, S., 2020. How mechanistic modelling supports decision making for the control of enzootic infectious diseases. *Epidemics* 32, 100398. <https://doi.org/10.1016/j.epidem.2020.100398>.
- Ferguson, N.M., Donnelly, C.A., Anderson, R.M., 2001. The foot-and-mouth epidemic in Great Britain: pattern of spread and impact of interventions. *Science* 292, 1155–1160. <https://doi.org/10.1126/science.1061020>.
- Froehly, J.L., Beane, N.R., Evans, D.E., Cagle, K.E., Jachowski, D.S., 2020. Using multiscale behavioural investigations to inform wild pig (*Sus scrofa*) population management. *PLoS ONE* 15 (2), e0228705. <https://doi.org/10.1371/journal.pone.0228705>.
- Giménez-Anaya, A., Bueno, C.G., Fernández-Llario, P., Fonseca, C., García-González, R., Herrero, J., Rosell, C., 2020. What do we know about wild boar in Iberia? In: Angelici, F.M., Rossi, L. (Eds.), *Problematic Wildlife II*. Springer, pp. 251–271. <https://doi.org/10.1007/978-3-030-42335-3>.
- Gneiting, T., Raftery, A.E., 2007. Strictly proper scoring rules, prediction, and estimation. *J. Am. Stat. Assoc.* 102, 359–378.

- Hayama, Y., Shimizu, Y., Murato, Y., Sawai, K., Yamamoto, T., 2020. Estimation of infection risk on pig farms in infected wild boar areas - epidemiological analysis for the reemergence of classical swine fever in Japan in 2018. *Prev. Vet. Med.* 175, 104873 <https://doi.org/10.1016/j.prevetmed.2019.104873>.
- Hayes, B.H., Andraud, M., Salazar, L.G., Rose, N., Vergne, T., 2021. Mechanistic modelling of African swine fever: a systematic review. *Prev. Vet. Med.* 191, 105358 <https://doi.org/10.1016/j.prevetmed.2021.105358>.
- James, L.P., Salomon, J.A., Buckee, C.O., Menzies, N.A., 2021. The use and misuse of mathematical modeling for infectious disease policymaking: lessons for the COVID-19 pandemic. *Med. Decis. Mak.* 41 (4), 379–385. <https://doi.org/10.1177/0272989x21990391>.
- Jamroz, M., Kolinski, A., Kihara, D., 2016. Ensemble-based evaluation for protein structure models. *Bioinformatics* 32 (12), i314–i321. <https://doi.org/10.1093/bioinformatics/btw262>.
- Johansson, M.A., Apfeldorf, K.M., Dobson, S., Devita, J., Buczak, A.L., Baugher, B., Moniz, L.J., Bagley, T., Babin, S.M., Guven, E., Yamana, T.K., Shaman, J., Moschou, T., Lothian, N., Lane, A., Osborne, G., Jiang, G., Brooks, L.C., Farrow, D.C., Hyun, S., Tibshirani, R.J., Rosenfeld, R., Lessler, J., Reich, N.G., Cummings, D.A.T., Lauer, S.A., Moore, S.M., Clapham, H.E., Lowe, R., Bailey, T.C., García-Díez, M., Carvalho, M.S., Rodó, X., Sardar, T., Paul, R., Ray, E.L., Sakrejda, K., Brown, A.C., Meng, X., Osoba, O., Vardavas, R., Manheim, D., Moore, M., Rao, D.M., Porco, T.C., Ackley, S., Liu, F., Worden, L., Convertino, M., Liu, Y., Reddy, A., Ortiz, E., Rivero, J., Brito, H., Juarrero, A., Johnson, L.R., Gramacy, R.B., Cohen, J.M., Mordecai, E.A., Murdock, C.C., Rohr, J.R., Ryan, S.J., Stewart-Ibarra, A.M., Weikel, D.P., Jutla, A., Khan, R., Poultney, M., Colwell, R.R., Rivera-García, B., Barker, C.M., Bell, J.E., Biggerstaff, M., Swerdlow, D., Mier-y-Teran-Romero, L., Forshey, B.M., Trtanj, J., Asher, J., Clay, M., Margolis, H.S., Hebbeler, A.M., George, D., Chretien, J.P., 2019. An open challenge to advance probabilistic forecasting for dengue epidemics. *Proc. Nat. Acad. Sci. USA* 116, 24268–24274. <https://doi.org/10.1073/pnas.1909865116>.
- Kao, R.R., 2002. The role of mathematical modelling in the control of the 2001 FMD epidemic in the UK. *Trends Microbiol* 10, 279–286. [https://doi.org/10.1016/s0966-842x\(02\)02371-5](https://doi.org/10.1016/s0966-842x(02)02371-5).
- Keeling, M.J., Woolhouse, M.E., Shaw, D.J., Matthews, L., Chase-Topping, M., Haydon, D.T., Cornell, S.J., Kappey, J., Wilesmith, J., Grenfell, B.T., 2001. Dynamics of the 2001 UK foot and mouth epidemic: stochastic dispersal in a heterogeneous landscape. *Science* 294, 813–817. <https://doi.org/10.1126/science.1065973>.
- Koopman, J.S., Simon, C.P., Getz, W.M., Salter, R., 2021. Modeling the population effects of escape mutations in SARS-CoV-2 to guide vaccination strategies. *Epidemics* 36, 100484. <https://doi.org/10.1016/j.epidem.2021.100484>.
- Korennoy, F.I., Gulenkin, V.M., Malone, J.B., Mores, C.N., Dudnikov, S.A., Stevenson, M. A., 2014. Spatio-temporal modeling of the African swine fever epidemic in the Russian Federation, 2007–2012. *Spat. Spatio-Tempo Epidemiol.* 11, 135–141. <https://doi.org/10.1016/j.sste.2014.04.002>.
- Lange, M., 2015. Alternative control strategies against ASF in wild boar populations. *EFSA Support. Publ.* 29. <https://doi.org/10.2903/sp.efsa.2015.EN-843>. EN-843.
- Lange, M., Thulke, H.-H., 2017. Elucidating transmission parameters of African swine fever through wild boar carcasses by combining spatio-temporal notification data and agent-based modelling. *Stoch. Environ. Res. Risk Assess.* 31, 379–391. <https://doi.org/10.1007/s00477-016-1358-8>.
- Leutbecher, M., Palmer, T.N., 2008. Ensemble forecasting. *J. Comput. Phys.* 227 (7), 3515–3539. <https://doi.org/10.1016/j.jcp.2007.02.014>.
- Luskin, M.S., Meijaard, E., Surya, S., Sheherazade, Walzer, C., Linkie, M., 2021. African swine fever threatens Southeast Asia's 11 endemic wild pig species. *Conserv. Lett.* 14, e12784 <https://doi.org/10.1111/conl.12784>.
- Marbach, D., Costello, J., Küffner, R., et al., 2012. Wisdom of crowds for robust gene network inference. *Nat. Methods* 9, 796–804. <https://doi.org/10.1038/nmeth.2016>.
- McCabe, R., Donnelly, C.A., 2021. Disease transmission and control modelling at the science–policy interface. *Interface Focus* 11, 20210013. <https://doi.org/10.1098/rsif.2021.0013>.
- McGowan, C.J., Biggerstaff, M., Johansson, M., Apfeldorf, K.M., Ben-Nun, M., Brooks, L., Convertino, M., Erraguntla, M., Farrow, D.C., Freeze, J., Ghosh, S., Hyun, S., Kandula, S., Lega, J., Liu, Y., Michaud, N., Morita, H., Niemi, J., Ramakrishnan, N., Yang, W., 2019. Collaborative efforts to forecast seasonal influenza in the United States, 2015–2016. *Sci. Rep.* 9, 2015–2016. <https://doi.org/10.1038/s41598-018-36361-9>.
- Metcalfe, C.J.E., Edmunds, W.J., Lessler, J., 2015. Six challenges in modelling for public health policy. *Epidemics* 10, 93–96. <https://doi.org/10.1016/j.epidem.2014.08.008>.
- Miguel, E., Grosbois, V., Caron, A., Pople, D., Roche, B., Donnelly, C.A., 2020. A systemic approach to assess the potential and risks of wildlife culling for infectious disease control. *Commun. Biol.* 3, 353. <https://doi.org/10.1038/s42003-020-1032-z>.
- Muñoz, F., Pleydell, D.R.J., Jori, F., 2022. A combination of probabilistic and mechanistic approaches for predicting the spread of African swine fever on Merry Island. *Epidemics* 40, 100596. <https://doi.org/10.1016/j.epidem.2022.100596>.
- Nigsch, A., Costard, S., Jones, B.A., Pfeiffer, D.U., Wieland, B., 2013. Stochastic spatio-temporal modelling of African swine fever spread in the European Union during the high risk period. *Prev. Vet. Med.* 108, 262–275. <https://doi.org/10.1016/j.prevetmed.2012.11.003>.
- Picault, S., Vergne, T., Mancini, M., Bareille, S., Ezanno, P., 2022. The African swine fever modelling challenge: objectives, model description and synthetic data generation. *Epidemics* 40, 100616. <https://doi.org/10.1016/j.epidem.2022.100616>.
- Probert, W.J.M., Shea, K., Fonnesbeck, C.J., Runge, M.C., Carpenter, T.E., Dürr, S., Garner, M.G., Harvey, N., Stevenson, M.A., Webb, C.T., Werkman, M., Tildesley, M. J., Ferrari, M.J., 2016. Decision-making for foot-and-mouth disease control: objectives matter. *Epidemics* 15, 10–19. <https://doi.org/10.1016/j.epidem.2015.11.002>.
- Reich, N.G., Brooks, L.C., Fox, S.J., Kandula, S., McGowan, C.J., Moore, E., Osthus, D., Ray, E.L., Tushar, A., Yamana, T.K., Biggerstaff, M., Johansson, M.A., Rosenfeld, R., Shaman, J., 2019. A collaborative multiyear, multimodel assessment of seasonal influenza forecasting in the United States. *Proc. Natl. Acad. Sci. USA* 116, 3146–3154. <https://doi.org/10.1073/pnas.1812594116>.
- Riordan, P., Delahay, R.J., Cheeseman, C., Johnson, P.J., Macdonald, D.W., 2011. Culling-induced changes in badger (*Meles meles*) behaviour, social organisation and the epidemiology of bovine tuberculosis. *PLoS ONE* 6, 28904. <https://doi.org/10.1371/journal.pone.0028904>.
- Sánchez-Cordón, P.J., Nunez, A., Neimanis, A., Wikström Lassa, E., Montoya, M., Crooke, H., Gavier Widén, D., 2019. African swine fever: disease dynamics in wild boar experimentally infected with ASFV isolates belonging to genotype I and II. *Viruses* 11 (9), 852. <https://doi.org/10.3390/v11090852>.
- Stegeman, A., Bouma, A., de Jong, M.C.M., 2010. Use of epidemiologic models in the control of highly pathogenic Avian influenza. *Avian Dis.* 54, 707–712. <https://doi.org/10.1637/8821-040209-Review.1>.
- Vergne, T., Korennoy, F., Combelles, L., Gogin, A., Pfeiffer, D.U., 2016. Modelling African swine fever presence and reported abundance in the Russian Federation using national surveillance data from 2007 to 2014. *Spat. Spatio-Tempo Epidemiol.* 19, 70–77. <https://doi.org/10.1016/j.sste.2016.06.002>.
- Vergne, T., Chen-Fu, C., Li, S., Cappelle, J., Edwards, J., Martin, V., Pfeiffer, D.U., Fusheng, G., Roger, F.L., 2017. Pig empire under infectious threat: risk of African swine fever introduction into the People's Republic of China. *Vet. Rec.* 181 (5), 117. <https://doi.org/10.1136/vr.103950>.
- Viboud, C., Vespignani, A., 2019. The future of influenza forecasts. *Proc. Natl. Acad. Sci. USA* 116 (8), 2802–2804. <https://doi.org/10.1073/pnas.1822167116>.
- Viboud, C., Sun, K., Gaffey, R., Ajelli, M., Fumanelli, L., Merler, S., Zhang, Q., Chowell, G., Simonsen, L., Vespignani, A., 2018. The RAPIDD ebola forecasting challenge: synthesis and lessons learnt. *Epidemics* 22, 13–21. <https://doi.org/10.1016/j.epidem.2017.08.002>.
- Webb, C.T., Ferrari, M., Lindström, T., Carpenter, T., Dürr, S., Garner, G., Jewell, C., Stevenson, M., Ward, M.P., Werkman, M., Backer, J., Tildesley, M., 2017. Ensemble modelling and structured decision-making to support emergency disease management. *Prev. Vet. Med.* 138, 124–133. <https://doi.org/10.1016/j.prevetmed.2017.01.003>.
- Woodroffe, R., Donnelly, C.A., Jenkins, H.E., Johnston, W.T., Cox, D.R., Bourne, F.J., Cheeseman, C.L., Delahay, R.J., Clifton-Hadley, R.S., Gettinby, G., Gilks, P., Hewinson, R.G., McInerney, J.P., Morrison, W.I., 2006. Culling and cattle controls influence tuberculosis risk for badgers. *Proc. Natl. Acad. Sci.* 103 (40), 14713–14717. <https://doi.org/10.1073/pnas.0606251103>.
- Yoo, D.S., Kim, Y., Lee, E.S., Lim, J.S., Hong, S.K., Lee, I.S., Jung, C.S., Yoon, H.C., Wee, S.H., Pfeiffer, D.U., Fournié, G., 2021. Transmission dynamics of African swine fever virus, South Korea, 2019. *Emerg. Infect. Dis.* 27, 1909–1918. <https://doi.org/10.3201/eid2707.204230>.
- Han, J.-H., Vignes, M., sub. 2022. A stochastic compartmental grid-based model for the Merry Island 2020 ASF outbreak Challenge. Submitted to the special issue ASF Modelling Challenge of Epidemics.