Multiple species animal movements: network properties, disease dynamics and the impact of targeted control actions

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Abstract
Infectious diseases in livestock are well-known to infect multiple hosts and persist through a combination of within- and between-host transmission pathways. Uncertainty remains about the epidemic dynamics of diseases being introduced on farms with more than one susceptible host species. Here, we describe multi-host contact networks and elucidate the potential of disease spread through farms with multiple hosts. Four years of between-farm animal movement among all farms of a Brazilian state were described through a static and monthly snapshot of network representations. We developed a stochastic multilevel model to simulate scenarios in which infection was seeded into single host and multi-host farms to quantify disease spread potential, and simulate network-based control actions used to evaluate the reduction of secondarily infected farms. We showed that the swine network was more connected than cattle and small ruminants in both the static and monthly snapshots. The small ruminant network was highly fragmented, however, contributed to interconnecting farms, with other hosts acting as intermediaries throughout the networks. When a single host was initially infected, secondary infections were observed across farms with all other species. Our stochastic multi-host model demonstrated that targeting the top 3.25% of the farms ranked by degree reduced the number of secondarily infected farms. The results of the simulation highlight the importance of considering multi-host dynamics and contact networks while designing surveillance and preparedness control strategies against pathogens known to infect multiple species.

Introduction
Infectious diseases in livestock populations have the potential to create large outbreaks and epidemics which compromise animal health and welfare, and produce economic losses [1]. Historically, these epidemics have been associated with disease transmission among multiple livestock hosts, i.e., the 2001 foot-and-mouth disease (FMD) outbreak in the United Kingdom [1]. To better understand the main drivers of such large-scale outbreaks, several studies have used social network analysis (SNA) and mathematical models to characterize animal movement patterns, often with a focus on individual food animal species such as cattle, [2–5] swine or small ruminants [6]. Only a few studies have developed mathematical models or even described contact networks over animal movement data of multiple species at the same time [7–16].

In previous literature, social network analysis has been used to shed light on between-farm disease spread processes, including the calculation of expected epidemic size where a wide range of network features derived from both static and monthly snapshots of network representation have been implemented [2, 17, 18]. The use of such approaches is very useful to describe the topology and temporal variation in the networks, however, it can lead to overestimation of the connectivity of the animal
trade. Therefore, approaches that account for the temporal order of movements such as temporal contact chains analysis and disease spread models have been successful in capturing epidemic trajectories [19–21].

The broader availability of animal movement data has been followed by significant advancements in disease spread modeling [22–24]. Those studies revealed important dynamic characteristics of epidemics that could be used in the development of targeted surveillance systems for farms with a higher likelihood of infection through animal movements [10, 25]. Our study was conducted with data from one Brazilian state. Here, we implemented analysis that allows for the description of the possible risks of animal movements, and identify key farms in the contact network using a multispecies approach. Social network analysis and mathematical models considering more than one host can deliver insights into the quantification of potential outbreak paths and provide useful data for the identification of key farms that can be used to break the direct contact transmission of animal diseases [8, 14, 26–29]. These insights are invaluable in supporting the design and implementation of efficient control and eradication strategies. From our detailed information about the entire movement data and population data, we aimed to: (i) characterize single-host and multi-host (bovine, swine and, small ruminants) contact networks across 4 years of movement data; (ii) examine the potential of disease spread from one specific host to a different host considering animal movements as a transmission route; and (iii) measure the impact of network-based target interventions to identify key nodes that could affect the number of infected premises in each host using a stochastic multi-level susceptible-infected model.

**Materials and methods**

Daily between-farm movement data from January 2015 to December 2018 of all registered farms with at least one of the following food animal hosts: cattle, buffalo, swine, sheep, or goat; were collected under a data use agreement with the Rio Grande do Sul Secretary of Livestock and Irrigation (SEAPI-RS, 2018) in Brazil. The spatial distribution of farms by host and municipalities by km² is presented in the Additional file 1. The data was extracted directly from the state’s database and included 1 621 374 movement records. Incomplete or inaccurate data including movements with missing farm identification, the same movement origin, and destination, or movements across state borders (n = 16 956) were not considered for the analysis. The final database included 1 604 418 movements and 90 090 619 animals; 944 records were fairs and events in farms corresponding to 467 nodes, which represents 0.16% of the total number of premises. Movements to slaughterhouses (34.56%, n = 554 487) were not included in the network description but were used in the disease spread model. For descriptive purposes cattle and buffalo hosts were grouped as “bovine”, and sheep and goat hosts were grouped as “small ruminants”.

**Static and monthly snapshots of networks representations**

The between-farm total of animals moved (referred herein as “batch”) was represented as a directed bipartite graph, g, where each farm was represented as a “node” and the movements between farms were represented as “edges”. Each edge has a specific node origin, i and a specific node destination, j. Each host network was analyzed individually and a full network (which includes all hosts) was reconstructed using data from all 4 years. Furthermore, in this static network description, node-level metrics: degree and, betweenness, were described by calculating the global mean with their respective confidence intervals of 95%, according to the network-host and period considered. The monthly snapshots of the static host networks of the full contact network were constructed to assess the temporal development of the network for the whole period of study using a monthly and yearly time resolution.

For both networks, we calculated network-level metrics including the number of nodes, edges, and animals; the diameter of the network; mean of degree; betweenness; PageRank; global cluster coefficient; and centralization based on degree. In addition, we also calculated the sizes of the connected components: Giant Strongly Connected Component (GSCC), and Giant Weakly Connected Component (GWCC) (Table 1). Based on the static network, the in-degree and out-degree distributions were calculated for each species and for the full network.

**Contact chains analysis**

We used contact chain analysis to describe the temporal and sequential nodes accessible by the formation of edges over time. These chains were divided into two main types: the in-going contact chains (ICC), which identify the number of farms that could potentially transmit the infection to the index farm over a defined period arising from the purchase and importation of animals; and the out-going contact chains (OCC), which can be used to quantify the number of farms that could potentially acquire infection from the index farm through the onward sale and export of animals [19, 30].

**Dynamic model description**

The proposed model was designed to demonstrate the potential for the spread of infectious animals from one specific host to a different host, considering only transmission through animal movements. We also measured
Within-farm dynamics

We implemented a discrete dynamic stochastic model that accounts for: (i) the local dynamics that represent each animal population (bovine, swine, and small ruminants); and (ii) the global dynamics that represent the interaction within farms and slaughterhouses; using a time resolution of 1 day. This transmission model framework is implemented using the *SimInf R* package for data-driven stochastic disease spread simulations [34] and the structure is described below.

Here, we tailored the within-farm dynamics to account for state transition from susceptible, \$S\$, to infected, \$I\$, compartments at a rate proportional to a frequency-dependent transmission coefficient, \$\beta = 0.7\$, in the simulated population. This assumed a homogeneously mixing population, \$i\$, within each premises where all hosts had identical rates of infection. The model considers the between-farm movements among farms of all species, therefore considering a real multi-host contact network.
of movement data from January 1st to December 31st, 2018. Of note, we did not explicitly model the heterogeneities related to animal space and geolocation, behavioral aspects, or animal categories such as age group for bovine or farm type in swine farms.

The initial simulation procedure was seeded in 1000 farms for each simulation. This was repeated so that each single-host farm or multi-host farm was the initial seeded farm for a total of 100 simulations. Transitions of animals between the susceptible and infected compartments were modeled as a continuous-time discrete-state using Gillespie’s direct method continuous-time Markov chain [34], as follows,

\[ \frac{dI}{dt} = \frac{\beta S_i I_i}{S_i + I_i}, \]

where \( t \) represents a specific time in a farm \( i \).

**Between-farm dynamics**

For the between-farm dynamics, susceptible farms, \( S_i \), can be infected by their contacts via daily animal movements. Within these dynamics, animal movements to a slaughterhouse destination were considered to be subtracting these animals from the system. The number of eligible animals moved between nodes and slaughterhouses were selected according to the daily movement records for each host. Each draw of animals from \( S \) and \( I \) compartments were at random, while the total number of available animals were based on the official data provided by [50] for each premises. To assure the stability of the farm populations, the animals born alive and declared to official veterinary service were used as an “enter event” and were assumed to be susceptible hosts. We subsequently calculated the number of ingoing and outgoing animals and the number of animals born and deceased for the full period of simulation, to update the animal population in each farm. For any site that has run out of animals, we reset the original number of animals reported to the state database [50]; this allows us to avoid sampling animals from non-existent populations. In Figure 1, we depict the interaction of the multiscale model considering both within-farm and between-farm dynamics. At the end of each simulation, the daily number of secondarily infected farms of each host was calculated.

**Simulating network-based targeted percolation**

Our analysis utilizes a theoretical percolation of farms (nodes) to remove nodes and their edges from the network [20, 35, 36]. Thus, these nodes are removed from the contact network as are all their associated animal movements, leading to a fragmented network that allows us to identify important farms whose removal reduces secondary infections.

We additionally considered the effect of sequential removal of farms from the network, based on their ranked order. Here, we used the static network constructed with movement data from 2015 to 2016, and the full network parameters of degree betweenness and PageRank (Table 1) to rank farms in descending order. We then quantify the effect of sequential removal on the reduction of secondarily infected farms in the host populations.

Furthermore, a sample of nodes was generated to be removed to simulate the non-targeted implementation of control actions from 2017 to 2018. The targeted farms were removed before model simulation was started to fragment the contact network, and the number of infected farms was then calculated at the end of each full simulation, on day 730 (December 31st, 2018). For each simulation, the number of secondarily infected farms was grouped by host species and network metric, and utilized in the identification of the key nodes to target with control actions. In this analysis, the “without control” scenario is represented as having zero nodes removed from the network since it represents the total number of infected farms observed when no control actions have been implemented. In the subsequent “with control” scenarios, all the simulations started with values taken from the end of the “without control” scenario, after which \( n \) nodes (ranging from 1 to 10,000) were removed and the impact over the number of secondary cases measured.

**Initial conditions and farm selection**

Since one of our objectives was to quantify the potential of a given infected host infecting another susceptible host(s) via animal transport, we developed scenarios A to C where the infection was seeded at bovine, small ruminants, and swine single host farms, respectively. Transportation of infected animals across multi-host farms was the only mode of disease propagation into other host species sites. In scenario D, infections were seeded in multi-host farms with at least two species (e.g. bovine and swine), and in scenario E, farms were randomly selected from the full network and seeded (Table 2). Each simulation started with 1000 infected farms drawn randomly from the farm list as the initially-seeded infections according to the model scenario (Table 2) and repeated 1000 times. In each initial infected farm, 10% of the animal population was assumed to be infected. Finally, the distribution of the number of secondarily infected farms at 5, 10, 15, and 30 days of the simulation was analyzed and presented according to the proposed list of scenarios (Table 2).
For the network-based targeted percolation analysis, we created three scenarios: (i) infection starting at bovine farms; (ii) infection starting at swine farms, and (iii) infection starting at small ruminant farms. For each scenario, we initiated each simulation infecting 1000 random farms with a within-farm prevalence of 10% similar
to the procedure described above. In each proposed scenario, we ran the model without removing any node for 100 simulations and then quantified the mean and the confidence interval of the number of secondarily infected farms. We then selected one farm to be removed from the full network, according to a farm-ranked list based on a specific network metric, and again ran 100 simulations to calculate the mean and the confidence interval of the number of secondarily infected farms. We repeated this procedure by increasing the number of removed farms by one until 10,000 farms were removed. Therefore, each scenario resulted in over a total of 1 million unique and individual simulations which are independent of other simulations.

Results

The total number of between-farm cattle and buffalo (bovine) movements were 1,251,615 (78.01%) batches and 20,773,516 (24.3%) animals, swine were 273,223 (17.02%) batches and 62,292,763 (72.8%) animals, and small ruminants represented 96,398 (6%) batches and 2,731,304 (2.89%) animals.

Bovine farms had the highest number of farms in the network followed by small ruminants and swine. For multi-host farms, the largest proportion was bovine and small ruminants with 10%, swine and bovine with 3.13%, all three host species with 0.37%, and swine and small ruminants with 0.04% (Figure 2A). Overall for the between-farm movements, bovine-to-bovine (41.5%) movements were the highest, however, 27.6% of small ruminant movements were between farms with bovine, followed by swine-bovine movements with 12.83%, swine-swine movements with 8.42%, small ruminant-to-small ruminant movements 7.95% and small ruminant-to-swine movements with 1.7% (Figure 2B and Additional file 2).

Static network description

As expected, bovine networks had the largest number of edges (Table 3). Mean betweenness was dominated by bovine and swine farms, while the clustering coefficient remained similar among all host species and centralization was significantly higher among swine farms (Table 3). When we compared the size of GWCC and GSCC, bovine farms had the largest connected components followed by small ruminants and swine. Similar patterns were found in the yearly temporal window presented in Additional file 3.

Distribution of in- and out-degree per host

In Figure 3, in- and out-degree distributions are presented individually for each host network. In general, for the full network, in-degree was higher than out-degree for bovine and small ruminants, while the swine network

![Figure 2](image-url)  
**Figure 2** Farm population and movements among hosts. **A.** Venn diagram of the number of farms and the proportion of farms among the three host groups. **B.** Circular plot for intra- and inter-host movement flows. Each external sector of the circle represents the origin of the movements where the numbers represent the total of the in-going and out-going movements for each host according to the number of interactions. The out-going animal flow starts from the base of each sector.
results indicate that after a degree value of 34 the frequency of out-degree was higher than in-degree.

### Monthly snapshots of networks representations

The monthly network representations are shown in Figure 4. The movements between swine farms have the highest mean degree, while bovine dominate in nodes, edges, and diameter throughout the four years. As expected the swine monthly-snapshot network exhibited a higher number of animals per batch than the other species. The calculated mean betweenness showed three unusual peaks for the bovine monthly-snapshot network; these are related to 49 nodes all associated with fairs, events, and exportation ports of bovine exportation, each one with betweenness values greater than 100 000 during the peak months, presented in Additional file 4. Small ruminant networks were steady throughout the four years. When evaluating the cluster coefficients, bovine and swine movements remain steady while small ruminants have large fluctuations. The swine network centralization was much higher than bovine or small ruminants, which could be related to how the industry is organized with the formation of groups of producers with commercial contracts with an integrator [21, 37]. For the GSCC and GWCC, the bovine monthly-snapshot network followed the same temporal patterns with the nodes indicating an important dependency in the number of active farms, while small ruminants showed the lowest values but with a temporal trend with higher values distributions in December and January. All results are presented in Additional files 5 and 6.

### Contact chains

The out-going contact chain (OCC) of the full network and the bovine network had similar distributions ranging from 10 to 10 000 farms. The OCC distribution for small ruminants showed a lower interquartile range when compared with the other distributions, while the swine OCC showed the largest interquartile range with higher densities in values above 100 farms (Figure 5).

The in-going contact chain (ICC) of bovine, swine, and small ruminant distributions follows a similar pattern of OCC counterparts, however, with lower distribution sizes. Bovine and small ruminants follow the same pattern, with values clustered between $10^4$ to $10^6$ (Figure 6). However, the contact chains for swine present very differently for both ICC and OCC compared to other hosts, with a wider interquartile range indicating larger chains to a wider range of farms. The highest density in the swine OCC was centered within 100 and 900 values, indicating a larger number of connected farms within that range (Figures 5 and 6).

### Assessment of secondary cases by host

Simulations were divided by their initial seed infection conditions according to the model scenarios A, B, C, and D. The estimated secondary cases, represented by the number of farms for the first 5, 10, 15, and 30 days of the disease propagation, are shown in Figure 7. For all simulated scenarios, secondary infections were observed across all host species. As expected, the highest number of infected farms corresponds to the species where the infection began due to most of the connections being intra-host. However, the connections

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### Table 3  Static network for cattle, swine, small ruminants, and for the full network

| Host          | Nodes | Edges | Mean degree (CI95%) | Diameter | Animals | GCC (%) | GWCC (%) | Mean betweenness (CI 95%) | Clustering coefficient | Network centralization |
|---------------|-------|-------|---------------------|----------|---------|---------|----------|---------------------------|------------------------|-----------------------|
| Swine         | 13,141| 75,205| 11.4 (10.99–11.90)  | 20       | 62,292,763 | 1885 (14.34%) | 9788 (74.34%) | 629,319 (477,380–781,257) | 0.032                  | 0.219                 |
| Cattle        | 261,892| 840,824| 6.4 (6.36–6.48)     | 33       | 20,773,716 | 105,609 (40.33%) | 249,742 (95.36%) | 712,451 (670,851–754,051) | 0.025                  | 0.003                 |
| Small ruminants| 32,325| 51,848| 3.2 (3.12–3.27)     | 26       | 1,763,834  | 5301 (16.40%)  | 25,420 (78.64%) | 33,394 (29,706–36,821)      | 0.028                  | 0.004                 |
| Full network  | 277,004| 1,038,346| 7.12 (7.05–7.18)    | 30       | 90,090,619 | 121,975 (44.03%) | 264,908 (95.63%) | 772,436 (706,188–785,513) | 0.03                   | 0.003                 |
between different hosts across multi-host farms made disease propagation to other hosts possible. It is important to note that large variabilities were observed in the distributions of swine farms followed by small ruminants and bovine, respectively. Furthermore, when simulations of the infection started in swine or small ruminants farms, there were no secondary infections between 5 to 30 days, which could be due to saturation of the current animal movement connections. A longer duration of time would be needed for farms to create movement connections with new farms.

The results are also presented as prevalence in Additional file 7, to allow for a comparison of the prevalence between each host. The prevalence is proportional to the number of farms per host, as the prevalence corresponds to the number of infected host farms divided by the number of farms that had at least one host species. Under these model considerations, swine farms were the most infected species when simulations started in multi-host farms. Moreover, the prevalence of small ruminants was higher than bovine for the majority of simulations with the exception of simulations that started at bovine farms. For bovine farms, when the simulation began in any other species, results showed the lowest prevalence of all hosts (Additional file 7). Additionally, in Additional file 8, we show the descriptive statistics for the farm prevalence in the 5, 10, 15, 30 days of spread disease simulation and total mean prevalence for each month by host and year starting at all random hosts in Additional file 9.

Effectiveness of network-based targeted percolation

Based on the simulation and subsequent theoretical removal of farms in the full network, the most effective network centrality metric throughout all hosts was the degree, followed by betweenness and PageRank, respectively. In Figure 8, the area of each color represents the number of infected farms on the last simulation day (December 31st, 2018) after performing the control action, which involved selecting \( n \) number of farms to be removed according to their ranked network metrics. The nodes were removed from the total population, and subsequently, the prevalence in each host was quantified. For example, in the swine panel, Figure 8, it is evident that random node removal from the total farm population is not efficient to break the full network and in consequence, could not reduce the swine farms prevalence since the removed nodes are not related to the pig farms’ connections. Whilst, the removal of 1000 farms ranked by degree was sufficient to reduce prevalence values close to zero in swine farms, for small ruminants and bovine it was not possible to reach close to zero infected farms, even with
10,000 farms removed from the networks. For bovine farms, the removal of 10,000 farms induced a reduction in prevalence from 5% to 1% (Figure 8 on the right y-axis). The list of the top 10,000 farms ranked by degree includes 5,316 bovine farms, 4,080 multi-host farms, 418 swine farms, and 43 small ruminant farms.

**Discussion**

In this study, we described between-farm contact networks of individual host species and a full network considering movements among bovine, small ruminants, and swine farms in one Brazilian state. Using the full network we developed a compartmental network model...
Figure 5  Boxplots and violin plots of the distribution of the yearly out-going contact chains by host and for the full network.

Figure 6  Boxplots and violin plots of the distribution of the yearly in-going contact chains by host and for the full network.
to assess the potential for disease spread through the contact networks while considering the implications of network-based control actions. Based on our descriptive analysis, we found higher connectivity in the static bovine network, while in the monthly snapshot network representations and the contact chains analysis we found higher connectivity in the swine network. In contrast, small ruminant farms were found to be widely disconnected in all network views, monthly snapshot static networks representations, and contact chains analysis approaches. In the Susceptible-Infected stochastic multi-host model, where we seeded infection individually to each host species, results demonstrated that transmission to other host-species was not dependent on the initially seeded species. In addition, we simulated node-removal from the full network, by ranking farms based on their network measure (i.e. degree) and subsequently removing the first 10,000 farms, showing that ranking by degree would reduce the simulated prevalence by from 5 to 1% (Figure 8). Thus, we argue that it is sensible for disease control and surveillance programs that target pathogens capable of infecting multiple hosts, to consider both the usual movement restrictions during disease emergencies, but also surveillance activities such as serosurveillance at all susceptible species. This is particularly relevant for foreign animal disease preparedness activities such as against FMD.

In the static network view, bovine networks accounted for 80.97% of the total movements and constituted 94.54% of farms in the database, generating the largest giant connected component sizes (GSCC and GWCC) and network diameter (Table 2). Within the full network, bovine farms acted as hubs that influenced the network dynamics by creating the presence of possible super spreader nodes such as event farms with a high out-degree, which has been described in other studies performed in Brazil [3–5]. In the current study, fairs and events movements represented only 0.16% of the total volume of all transported animals, which differed greatly from movement patterns in other countries such as in the UK where 30.4% of movements were related to movements to markets [38]. In the monthly snapshot network representations view, the swine network was more connected than all other host species, with higher values of animal movements, mean of degree, centralization, and giant connected component percentages. This is likely because of the pyramidal structure commercial pig production utilizes to improve performance and productivity. Because of such continuous flow, nurseries and wean to finishers tend to receive and send a great number of pigs, thus have a higher degree in comparison with other production types [21, 37, 39]. In contrast, the network connectivity in bovine farms was low despite having more than 20,000 edges and high node activity in a
monthly view. This result was noticeable by the distribution of the degree parameter, in which all hosts exhibited power-law distributions, suggesting that these networks are characterized as scale-free [19, 40]. Additionally, the degree distribution results could help highlight super-spreaders in all host populations through the identification of farms with several commercial partners that make a major contribution to disease spread [41]. For example, the swine network was highlighted as the network with the largest degree, which has been described previously in the same region [2, 21]. Finally, the analysis of the small ruminant networks showed a very disconnected network with a marked seasonality at the end of each year but with fewer monthly edges and nodes than

![Network metrics](image_url)
swine and cattle farms, despite having more registered farms than the swine production in the full network.

Our modeling results showed that regardless of which species was first infected at the beginning of the simulations, secondary infections were detected in all farm types. This indeed is likely associated with the network structure and how food animal populations and production are organized in the study region. However, to the author’s knowledge, this is the first in-depth characterization of a multi-host animal networks in Brazil. We argue that uncovering the interconnection among multiple species is of great relevance because most disease control programs are centered in only a single species, often neglecting the potential of disease introduction from a different host species (e.g. FMD, influenza).

When infection started in multi-host farms the distribution of the final number of infected farms at the end of the simulation, bovine farms had a higher median than the other species, while the swine farms showed broader distributions compared to small ruminants and bovines. This may be explained mainly by how commercial pig production is organized, often extremely vertically integrated with a high volume of pigs moving from farm-to-farm based on age/production phases. Finally, in all scenarios with simulations seeded in a single host (i.e. swine) the estimated number of infected farms at 30 days post-seeded infection was higher than the simulations which seeded infection in the multi-host farms. This is because the connectivity of single host farm networks allows for the spread of disease quickly, infecting more farms of the specific host species in the 30-day time frame than when the disease is started in a multi-host farm. Similar patterns have been observed in past epidemics, such as the FMD [14, 15, 26, 42, 43] where multi-host farms had a role in infection propagation.

We used our proposed model to also simulate network-based interventions, thus we used node-removal strategies to test control actions. Targeting and removing farms sequentially based on network metrics, was most impactful when the degree was used. This reduced the expected number of infected farms from ~5% to ~1% in the bovine network (degree), 0.6% to ~0.01 in the swine network (degree), and ~1 to ~0.025% in the small ruminant network (degree). In contrast, random node removal was the least efficient in reducing secondary infections. An unexpected result was that for small ruminants, random removal of nodes had a better impact in reducing transmission than using PageRank network metric, partly because this network is more disconnected compared to the other host-networks which leads to PageRank failing to recognize important farms for the spread of disease. Previous studies that also utilized large datasets and similar node-removal approaches but in single host networks, reported similar results as ours, especially for bovine networks [33, 35, 44, 45] and swine networks [21, 37, 41]. Studies that considered more than one host species and network-based target control actions reported a larger reduction in the expected number of cases directly generated by one case in a population, size of the connected components, and the number of infected farms using degree-based interventions [10, 14]. An important limitation of the studies listed above is the use of static networks which could have overestimated the connectivity of those networks [14, 20, 45]. Therefore, we argue for the need to consider temporal models, such as our contact chain analysis, when developing network-based target approaches, because it considers the temporal order of the connections and avoids over-connectivity of the static networks [20, 45]. Furthermore, network analysis approaches have been widely used recently; the great majority centered on describing the contact networks of a single species, here we cite just some relevant examples [2, 18, 32, 39, 40, 46–48], however, only a fraction of studies have explicitly considered the interaction of possible contacts among more than one species while constructing their transmission networks [7–9, 11–13, 15, 16, 49]. While single host networks are informative, they are likely to underestimate the epidemic propagation of pathogens capable of infecting multiple species [26, 50–53]. Our results reinforce the relevance of including data, when available, of all susceptible host species while developing regional disease preparedness activities into disease surveillance systems and agree with previous literature which reported better performance of temporal network measures in identifying farms that could be targeted to reduce the secondary number of infections [39].

Limitations and further remarks

Our main goal in this study was to quantify the role of multi-host farms in disease transmission via contact networks and identify hubs in the networks. Therefore, while we are aware that fomites such as delivery trucks and local-area spread are important for disease propagation [50, 54], we have not included such transmission pathways in our model nor have we included the heterogeneity present in disease transmission for any specific disease. However, in future work, we will specifically set transmission coefficients for each host species (e.g. swine, cattle) interaction, and incorporate spatial transmission within a full network model to model, for example, the spread of FMD. Additionally, we did not consider animal level dynamics (i.e. age, commercial versus backyard swine farms) so the risk each animal posed for disease transmission was assumed to be the same, which could contribute to an overestimation of the transmission
potential. Similarly, this is not an individual-based model so we cannot individualize the results for a specific individual or calculate the time that an animal spends on each farm. Furthermore, we are unable to quantify the effect of other between-farm movements such as veterinarians and employees, which may contribute to the transmission through indirect contacts.

Using a stochastic network model, our results demonstrate that outbreaks starting in a particular host species resulted in outbreaks on farms with all other host species. Small ruminant farms, despite the lower number of nodes in the network, share a large number of contacts among other host-nodes in the full network. In addition, our multi-host network-based intervention model showed that identifying and deploying surveillance to the 10,000 farms with the largest degree, regardless of host species, would reduce more than 70% of the simulated transmission. Ultimately, this study helps to understand the temporal variation in between-farm movement fluctuations and the topology of each contact network, as well as the similarities and differences among the three species’ movement dynamics.

Abbreviations
FMD: foot and mouth disease; OVS: official veterinary service; SNA: Social Network analysis; GSCC: giant strongly connected components; GWCC: giant weakly connected components; ICC: in-going contact chains; OCC: out-going contact chains.

Supplementary Information
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Authors’ contributions
NCC and GM conceived the study. NCC and GM participated in the design of the study. FPNL coordinated the movement data collection. NCC conducted data processing, cleaning, designed the model, and simulated scenarios with the assistance of GM. NCC and GM designed the computational analysis. NCC conducted the formal coding. NCC, ALS, and GM wrote and edited the manuscript. GM secured the funding. All authors read and approved the final manuscript.

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Availability of data and materials
The data that support the findings of this study are not publicly available and are protected by confidential agreements, therefore, are not available. Spread disease simulation and node removal code are available in the repository: https://github.com/machado-lab/Multiple-species-animal-movements-network-properties-disease-dynamic-and-the-impact-of-targeted.

Declarations
Ethics approval and consent to participate
The authors confirm the ethical policies of the journal, as noted on the journal’s author guidelines page. Since this work did not involve animal sampling nor questionnaire data collection by the researchers, there was no need for ethics permits.

Consent for publication
All authors discussed the results and critically reviewed the manuscript to approve for publication.

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

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References
1. Davies G (2002) The foot and mouth disease (FMD) epidemic in the United Kingdom 2001. Comp Immunol Microbiol Infect Dis 25:331–343. https://doi.org/10.1016/S0147-9571(02)00030-9
2. Cardenas NC, Pozo P, Lopes FPN, Grisi-Filho JHH, Alvarez J (2021) Use of network analysis and spread models to target control actions for bovine tuberculosis in a state from Brazil. Microorganisms 9:227. https://doi.org/10.3390/microorganisms9020227
3. de Menezes TC, Luna I, de Miranda SHG (2020) Network analysis of cattle movement in Mato Grosso Do Sul (Brazil) and Implications for foot-and-mouth disease. Front Vet Sci 7:219. https://doi.org/10.3389/fvets.2020.00219
4. Negreiros RL, Grisi-Filho JHH, Dias RA, Ferreira F, Ferreira Neto JS, Ossada R, Amaku M (2020) Analysis of the cattle trade network in the state of Mato Grosso, Brazil. Braz J Vet Res Anim Sci 57:e171635. https://doi.org/10.11606/issn.1678-4456.bjvras.2020.171635
5. Silva Júnior JL, Almeida EC, Corrêa FN, Ossada R, Marques FS, Dias RA, Ferreira F, Neto JS, Gisi-Filho JHH, Amaku M, Manso Filho HC, Silva JCR (2017) Livestock markets play an important role in the cattle movement network in Pernambuco, Brazil. Braz J Vet Res Anim Sci 54:225. https://doi.org/10.11606/s1678-4456.bjvras.2017.124303

6. Kocho T, Abebe G, Tegegne A, Gebremedhin B (2011) Marketing value-chain of smallholder sheep and goats in crop-livestock mixed farming system of Alaba, Southern Ethiopia. Small Rumin Res 96:101–105. https://doi.org/10.1016/j.smallrumin.2011.01.008

7. Amparato L, Karg H, Roesser R, Provost J, Akoto-Danso EK, Sidibe S, Buerkert A (2020) Vehicular livestock mobility in West Africa: seasonal traffic flows of cattle, sheep, and goats across Bamako. Sustainability 13:171. https://doi.org/10.3390/su13010171

8. Cabezas AH, Sanderson MW, Lockhart CY, Riley KA, Hanthorn CJ (2021) Spatial and network analysis of U.S. livestock movements based on Interstate Certificates of Veterinary Inspection. Prev Vet Med 193:105391. https://doi.org/10.1016/j.prevetmed.2021.105391

9. Kao RR, Green DM, Johnson J, Kiss IZ (2007) Disease dynamics over very different time-scales: foot-and-mouth disease and scraep on the network of livestock movements in the UK. J Soc Interface 4:907–916. https://doi.org/10.1098/rsif.2007.1129

10. Marquetoux N, Stevenson MA, Wilson P, Rider A, Heuer C (2016) Using social network analysis to inform disease control interventions. Prev Vet Med 126:94–104. https://doi.org/10.1016/j.prevetmed.2016.01.022

11. Martínez-López B, Iborna V, Fernández-Carrion E, Perez AM, Medel-Herrero A, Sánchez-Vizcaíno F, Gortázar C, Ramos AM, Sánchez-Vizcaíno JM (2014) A multi-analysis approach for space–time and economic evaluation of risks related with livestock diseases: the example of FMD in Peru. Prev Vet Med 114:47–63. https://doi.org/10.1016/j.prevetmed.2014.01.013

12. Omondi GP, Obanda V, VanderWaal K, Deen J, Travis DA (2021) Animal movement in a pastoralist population in the Masai Mara Ecosystem in Kenya and implications for pathogen spread and control. Prev Vet Med 188:105259. https://doi.org/10.1016/j.prevetmed.2021.105259

13. Poonkhet C, Kasemsuwan S, Phiphakhamvong S, Phouangsoonvichan V, Vongkay K, Shin MS, Kalpravidh W, Hinrichs J (2019) Social network analysis for the assessment of pig, cattle and buffalo movement in Kayabouli, Lao PDR. PeerJ 6:e6177. https://doi.org/10.7717/peerj.6177

14. Ruget A-S, Rossi G, Pepler PT, Beaunée G, Banks CJ, Enright J, Kao RR (2021) Multi-species temporal network of livestock movements for disease spread. Appl Netw Sci 6:15. https://doi.org/10.1007/s41109-021-00354-x

15. Tildesley MJ, Keeling MJ (2008) Modelling foot-and-mouth disease: a comparison between the UK and Denmark. Prev Vet Med 85:107–124. https://doi.org/10.1016/j.prevetmed.2008.01.008

16. Valerio VC, Walther OJ, Eliittä M, Cissé B, Muneepeerakul R, Kiker GA (2020) Network analysis of regional livestock trade in West Africa. PLoS One 15:e0232681. https://doi.org/10.1371/journal.pone.0232681

17. Kao RR, Danon L, Green DM, Kiss IZ (2008) Demographic structure and pathogen dynamics on the network of livestock movements in Great Britain, Proc R Soc B Biol Sci 275:1999–2007. https://doi.org/10.1098/rspb.2006.3505

18. VanderWaal KL, Picasso C, Eva A, Craft ME, Alvarez J, Fernandez F, Girt A, Perez A, Wells S (2016) Network analysis of cattle movements in Uruguay: quantifying heterogeneity for risk-based disease surveillance and control. Prev Vet Med 133:1–22. https://doi.org/10.1016/j.prevetmed.2015.12.003

19. Fielding HR, McKinley T, Silk MJ, Delahay RJ, McDonald RA (2019) Contact chains of cattle farms in Great Britain. R Soc Open Sci 6:180719. https://doi.org/10.1098/rsos.180719

20. Lento HHH, Koher A, Hövel P, Gethmann J, Sauter-Louis C, Selhorst T (2020) Disease dynamics on the network of livestock movements in Great Britain: network properties and their implications for infection chains by targeted removal of central holdings in an animal trade network. PLoS One 15:e0232489. https://doi.org/10.1371/journal.pone.0232489

21. Cardenas NC, VanderWaal K, Veloso FP, Galvis JA, Prada JM, Machado G (2021) The between-farm transmission dynamics of porcine epidemic diarrhoea virus: a short-term forecast modelling comparison and the effectiveness of control strategies. Transbound Emerg Dis. https://doi.org/10.1111/tbed.13997 (in press)

22. Cauteren KC, Webb CT (2019) Modelling multi-species and multi-mode traffic during livestock disease outbreaks and for risk-based surveillance. BMC Vet Res 17:1. https://doi.org/10.1186/s12917-019-1863-7

23. Knific T, Ocepek M, Kirbiš A, Lentz HHK (2020) Implications of cattle trade network. PLoS One 8:e74292. https://doi.org/10.1371/journal.pone.0074292

24. Kiss IZ, Green DM, Kao RR (2006) The network of sheep movements within Great Britain: network properties and their implications for infectious disease spread. J R Soc Interface 3:669–677. https://doi.org/10.1098/rsif.2006.0129

25. Carreras X, Gallart X, Lluch A, Gillard E, Calla M, Weiss J, Ross M, Dessaint P, Viana M, Pujol J, Armengol J, de la Roza F, Espana J, Vives J, Madrona J, Romagnoli J, Antenas J, Baynat J, Cerdà G, Llovet J (2021) Predictive gravity models of livestock mobility in Mauritania: the effects of supply, demand and cultural factors. PLoS One 13:e0199547. https://doi.org/10.1371/journal.pone.0199547

26. Widgren S, Sauer P, Eriksson R, Engblom S (2019) SimIn: An R package for data-driven stochastic disease spread simulations. J Stat Softw 91:1–42. https://doi.org/10.18637/jss.v091.i12

27. Knific T, Ocepek M, Kirbiš A, Lentz HHK (2021) Spatio-temporal network analysis of pig trade to inform the wildlife–livestock interface. J Appl Ecol 56:1471–1481. https://doi.org/10.1111/1365-2664.13370

28. Isabel C, Ocepek M, Kirbiš A, Lentz HHK (2021) Spatio-temporal network analysis of pig trade to inform the wildlife–livestock interface. J Appl Ecol 58:100398. https://doi.org/10.1111/1365-2664.13370

29. Cardenas NC, VanderWaal K, Veloso FP, Galvis JA, Amaku M, Grisi-Filho JHH (2021) Spatio-temporal network analysis of pig trade to inform the design of risk-based disease surveillance. Prev Vet Med 189:105314. https://doi.org/10.1016/j.prevetmed.2021.105314

30. Robinson SE, Christley RM (2007) Exploring the role of auction markets in cattle movements within Great Britain. Prev Vet Med 81:21–37. https://doi.org/10.1016/j.prevetmed.2007.04.011

31. Passafaro TL, Fernandes AFA, Valente BD, Williams NH, Rosa GJM (2020) Network analysis of swine movements in a multi-site pig production system in Iowa, USA. Prev Vet Med 174:104856. https://doi.org/10.1016/j.prevetmed.2019.104856

32. Salinas M, Andraud M, Rose N (2017) Pig movements in France: designing network models fitting the transmission route of pathogens. PLoS One 12:e0185588. https://doi.org/10.1371/journal.pone.0185588
41. Alarcón LV, Cipriotti PA, Monterubbianesi M, Perfumo C, Mateu E, Allepuz A (2020) Network analysis of pig movements in Argentina: identification of key farms in the spread of infectious diseases and their biosecurity levels. Transbound Emerg Dis 67:1152–1163. https://doi.org/10.1111/tbed.13441

42. Firestone SM, Hayama Y, Lau MSY, Yamamoto T, Nishi T, Bradhurst RA, Demirhan H, Stevenson MA, Tsutsui T (2020) Transmission network reconstruction for foot-and-mouth disease outbreaks incorporating farm-level covariates. PLoS One 15:e0235660. https://doi.org/10.1371/journal.pone.0235660

43. Green DM, Kiss IZ, Kao RR (2006) Modelling the initial spread of foot-and-mouth disease through animal movements. Proc Biol Sci 273:2729–2735. https://doi.org/10.1098/rspb.2006.3648

44. Brown E, Marshall AH, Mitchell HJ, Byrne AW (2019) Cattle movements in Northern Ireland form a robust network: implications for disease management. Prev Vet Med 170:104740. https://doi.org/10.1016/j.prevetmed.2019.104740

45. Büttner K, Salau J, Krieter J (2016) Quality assessment of static aggregation compared to the temporal approach based on a pig trade network in Northern Germany. Prev Vet Med 129:1–8. https://doi.org/10.1016/j.prevetmed.2016.05.005

46. Büttner K, Krieter J (2021) Epidemic spreading in a weighted pig trade network. Prev Vet Med 188:105280. https://doi.org/10.1016/j.prevetmed.2021.105280

47. Duncan AJ, Reeves A, Gunn GJ, Humphry RW (2022) Quantifying changes in the British cattle movement network. Prev Vet Med 198:105524. https://doi.org/10.1016/j.prevetmed.2021.105524

48. Ezanno P, Annoux S, Joly A, Vermesse R (2022) Rewiring cattle trade movements helps to control bovine paratuberculosis at a regional scale. Prev Vet Med 198:105529. https://doi.org/10.1016/j.prevetmed.2021.105529

49. Nöremark M, Håkansson N, Lewerin SS, Lindberg A, Jonsson A (2011) Network analysis of cattle and pig movements in Sweden: measures relevant for disease control and risk based surveillance. Prev Vet Med 99:78–90. https://doi.org/10.1016/j.prevetmed.2010.12.009

50. Boender GJ, van Roermund HJW, de Jong MCM, Hagenaaars TJ (2010) Transmission risks and control of foot-and-mouth disease in The Netherlands: spatial patterns. Epidemics 2:36–47. https://doi.org/10.1016/j.epidem.2010.03.001

51. Chis Ster I, Dodd PJ, Ferguson NM (2012) Within-farm transmission dynamics of foot and mouth disease as revealed by the 2001 epidemic in Great Britain. Epidemics 4:158–169. https://doi.org/10.1016/j.epidem.2012.07.002

52. Halasa T, Ward MP, Boklund A (2020) The impact of changing farm structure on foot-and-mouth disease spread and control: a simulation study. Transbound Emerg Dis 67:1633–1644. https://doi.org/10.1111/tbed.13500

53. Payer A, Tabourier L, Latapy M (2019) Spreading dynamics in a cattle trade network: size, speed, typical profile and consequences on epidemic control strategies. PLoS One 14:e0217972. https://doi.org/10.1371/journal.pone.0217972

54. Yang Q, Gruenbacher DM, Heier Stamm JL, Amrine DE, Brase GL, DeLoach SA, Scoglio CM (2020) Impact of truck contamination and information sharing on foot-and-mouth disease spreading in beef cattle production systems. PLoS One 15:e0240819. https://doi.org/10.1371/journal.pone.0240819

55. Plowright W (1984) The duration of immunity in cattle following inoculation of rinderpest cell culture vaccine. J Hyg 92:285–296

56. Terpstra C, Van Maanen C, Van Bekkum JG (1990) Endurance of immunity against foot-and-mouth disease in cattle after three consecutive annual vaccinations. Res Vet Sci 49:236–242

57. Wasserman S, Faust K (1994) Social network analysis: methods and applications. Cambridge University Press, Cambridge

58. Brin S, Page L (1998) The anatomy of a large-scale hypertextual Web search engine. Comput Netw ISDN Syst 30:107–117. https://doi.org/10.1016/S0169-7552(98)00110-X

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