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Research paper

Phylogeographic analysis of the 2000–2002 foot-and-mouth disease epidemic in Argentina

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ABSTRACT

Foot-and-mouth disease (FMD) is a highly transmissible disease of hooved livestock. Although FMD has been eradicated from many countries, economic and social consequences of FMD reintroductions are devastating. After achieving disease eradication, Argentina was affected by a major epidemic in 2000–2002, and within few months, FMD virus spread throughout most of the country and affected >2500 herds. Available records and viral strains allowed us to assess the origins, spread and progression of this FMD epidemic, which remained uncertain. We used whole genome viral sequences and a continuous phylogeographic diffusion approach, which revealed that the viruses that caused the outbreaks spread fast in different directions from a central area in Argentina. The analysis also suggests that the virus that caused the outbreaks in the year 2000 was different from those found during the 2001 epidemic. To estimate if the approximate overall genetic diversity of the virus was related to disease transmission, we reconstructed the viral demographic variation in time using Bayesian Skygrid approach and compared it with the epidemic curve and the within-herd transmission rate and showed that the genetic temporal diversity of the virus was associated with the increasing number of outbreaks in the exponential phase of the epidemic. Results here provide new evidence of how the disease entered and spread throughout the country. We further demonstrate that genetic data collected during a FMD epidemic can be informative indicators of the progression of an ongoing epidemic.

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1. Introduction

Foot-and-mouth disease (FMD) is arguably one of the most important diseases of hooved livestock worldwide and it is endemic in many African and Asian countries (OIE, 2009). In South America, official disease status and effectiveness of control programs are disparate between countries, resulting in sporadic epidemics in disease-free areas. One of the most dramatic examples of this situation took place in 2000–2002, when a devastating FMD epidemic affected Argentina, few months after the country discontinued vaccination and was recognized as free-without vaccination by the International Organisation of Animal Health (OIE). There was an initial outbreak in August 2000 that was controlled using stamping out and movement control policy (Perez et al., 2004a). Unfortunately early in 2001, another introduction FMD virus (FMDV) serotype A, occurred, resulting in a total of 2519 herds affected throughout the country. This epidemic was finally controlled implementing massive vaccination, animal movement control, and active surveillance strategies (Perez et al., 2004b). However, there was a need to reformulate the vaccination strategy twice to incorporate the strains from 2000 (A/Arg/00) and 2001 (A/Arg/01) viruses (Mattion et al., 2004; Perez et al., 2004a). Since then, the country conducts mandatory vaccination campaigns twice a year nationwide, except in southern areas of Argentina, the only region in the country that has remained free from FMD. This large epidemic in Argentina was well documented and previous studies of this epidemic have been aimed at describing the epidemiological features (Perez et al., 2004b), molecular epidemiology (Konig et al., 2007; Perez et al., 2008), vaccine matching (Mattion et al., 2009), and within-herd transmission (Brito et al., 2011).

During the last decade, methods for analyzing sequences and using them to reveal epidemiologic aspects of infectious diseases based on genetic data of the pathogens, a field known as phylodynamics, have been rapidly emerging and evolving (Grenfell et al., 2004; Volz et al., 2013). Within this field, the reconstruction of the phylogeny and the geographical location of virus' ancestors, referred to as phylogeography has

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shown to have an important application to understand viral spread. Additionally, important information contained in the estimated phylogeny can be used to infer temporal changes in the viral genetic diversity (estimated by the effective viral population size). Previous studies have suggested that the increase of the viral population size or genetic diversity is related to an increase of disease incidence, and transmission rate of the virus due to the association between the coalescent rate and rate of transmission (Frost & Volz, 2010; Holmes et al., 1995). However, estimates of infectious diseases transmission rates normally rely on partial data obtained from a proportion of individuals reporting the disease, so the real incidence is approximated using different epidemiological tools. In the case of some animal diseases, reporting is mandatory, and clinical disease is evident in most cases, so animal health authority records allow having accurate information about disease occurrence. Such is the case of FMDV when introduced into a disease-free country.

The objective of the study here was to estimate the spread pattern of FMDV A/Arg/01 in one of the largest epidemics reported and documented in a disease-free country. We used Bayesian methods to reconstruct the phylogeny, and a random walk diffusion model to account for the spatial spread of the virus. We further determined the viral population size and compared it with the epidemic curve and the within-herd transmission rate of the FMD epidemic in Argentina in 2001. Results from the estimated viral population size obtained from sequence analysis suggest that this approach can be applied to detect the duration of the exponential growth of cases over the course of an epidemic.

2. Methods

2.1. Study population and sampling

Veterinarians of the National Argentine Veterinary Services (SENASA), visited all affected herds and collected samples from clinical lesions, as well as all data pertaining to herd demographics and diseased animals. Collected samples were stored at −70 °C. All records of infected herds were categorized into 3 different periods of the epidemic (exponential, saturation, and declining phase), and geographically in 3 different regions, as previously described (Perez et al., 2004b). Finally, thirty specimens from different time (epidemic periods) and geographical categories previously described (the number of sequences included from each epidemic period and geographic category was proportional to the number of outbreak events occurred within those categories), and which had a relatively high viral load were sequenced. All samples were collected in cattle, which was, almost exclusively, the only susceptible species affected during the epidemic.

Information of the computed intra-herd transmission coefficient (the rate at which a susceptible individual acquired the infection from an infected one) for every herd was available from our prior study (Brito et al., 2011).

2.2. RNA extraction, RT-PCR, and virus sequencing

Whole genome sequencing was performed at the National Institute of Agricultural Technology. Viral RNA was inactivated and extracted directly from the disrupted tissue (field samples) using Tri-Reagent® (MRC) according to the manufacturer's protocol. RNA was reverse transcribed into cDNA using 50 ng of random hexamer primers (Invitrogen), 2 pmol of specific reverse primer, and 400 U of MMLV-RT Superscript III (Invitrgoen) following the manufacturer's indications except for cDNA treatment with RNAse H (not performed). cDNA was used as template for the amplification of 7 overlapping fragments using Taq polymerase HiFi (Invitrogen). PCR tests were performed in order to amplify the complete genome in seven 0.4–2.0 kb-long PCR fragments. An automated Sanger sequencer was used for sequencing, obtaining a mean coverage of 3.75×. Finally, 30 complete genome sequences were obtained. All primers and conditions used to sequence this virus are available in (Appendix A). GenBank accession number and related information of the sequences are shown in Table 1.

Table 1
Location and collection date of sequences used in the study.

Sequence name	Collection date	Latitude	Longitude	GenBank accesion number
38950_For_Pat	12/31/00	−24.083	−60.375	KX002194
39064_SL_Ped	2/10/01	−34.250	−65.375	KX002195
39111_Cor_Gpaz	2/18/01	−27.917	−57.875	KX002196
AGLopez01	3/7/01	−33.750	−62.125	KX002204
AAreco01	3/13/01	−34.417	−59.625	KX002203
129_LPam_Capital	3/21/01	−36.750	−64.125	KX002178
ATLauquen01	3/27/01	−35.917	−62.875	KX002205
258_ER_Diamante	3/29/01	−32.083	−60.375	KX002193
423_Cor_Union	4/17/01	−32.083	−62.375	KX002197
467_SFe_Irio	4/20/01	−32.917	−61.375	KX002198
548_LP_Guatrech	4/26/01	−37.583	−63.375	KX002199
820_Cor_Groca	5/12/01	−34.583	−63.375	KX002200
915_SEst_Riv	5/15/01	−29.917	−62.125	KX002201
973_SL_Pede	5/15/01	−33.583	−65.375	KX002202
1155_BsAs_MCh	5/25/01	−37.417	−57.875	KX002176
1293_BsAs_Indio	5/28/01	−35.417	−57.625	KX002179
1185_ER_Par	5/28/01	−31.583	−59.875	KX002177
1300_BS_As_Gguido	6/3/01	−36.583	−57.875	KX002180
1441_BsAs_Lflores	6/16/01	−35.583	−59.125	KX002181
1452_longMCH	6/17/01	−37.417	−57.875	KX002182
1514_LPam_HU	6/17/01	−38.083	−64.125	KX002183
1893_longMCH	7/10/01	−37.417	−57.625	KX002184
2027_Cor_Col	7/20/01	−31.083	−63.875	KX002186
2026_Tuc_Tuc	8/7/01	−26.9165	−65.125	KX002185
2071_LPam_Chali	8/8/01	−36.750	−66.625	KX002189
2063_Cor_Ccuat	8/15/01	−29.583	−58.875	KX002188
2059_BsAs_Hirig	8/21/01	−36.083	−61.625	KX002187
2084_StEst_OjoAgua	9/1/01	−29.583	−63.125	KX002190
2107_BsAs_Merced	10/11/01	−34.583	−59.375	KX002191
2118_LPam_Lmahu	11/15/01	−36.917	−66.875	KX002192

2.3. Phylogenetic analysis

Sequences of the FMDV A/Arg/2001 whole genome were aligned using MUSCLE (Edgar, 2004) software. Previous to estimation of the phylogeny, we assessed virus recombination using the Recombinant Identification Program (Siepel et al., 1995). Recombination analysis is used to estimate the most appropriate phylogenetic analysis, and to understand the potential mechanisms that the virus uses to evolve (in this case to estimate whether this virus that caused a massive outbreak, was a recombinant). We used whole genome of FMDV A strains A/Arg/00 (previous strain that caused a smaller outbreak in Argentina in 2000, GenBank: AY593782), as well as A24 and A25 (vaccine viruses used in previous years, GenBank: AY593767, AY593769) to compare similarities and to establish potential recombination. We also assessed recombination among all the sequenced viruses in this study. This method searches at different sizes of regions within sequences, identifies similarities between these regions and test for potential recombination.

To obtain the topology of the phylogenetic tree and evolutionary parameters, we used Bayesian Evolutionary Analysis by Sampling trees (BEAST v1.8) (Drummond and Rambaut, 2007). We initially estimated independently the phylogeny of each of the 12 protein-coding segments. For each protein-coding segment alignment, we selected the best codon partition scheme and substitution model using PartitionFinder software (Lanfear et al., 2012), based on the Bayesian information criterion. Using the selected substitution model and partition scheme we reconstructed the phylogeny using two different clock models for each protein coding segment: the strict clock and the uncorrelated lognormal relaxed clock (ucln) model. The (mean) clock rate for each protein was used to determine if different proteins differed in their evolution rate. The rates estimated were later used as informative initial values to set the multilocus analysis for the whole genome. For

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