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3 authors:

Keith Sumption
Food and Agriculture Organization of the United Nations

Mark Rweyemamu
Southern African Centre for Infectious Disease Surveillance

William Wint
University of Oxford

ORIGINAL ARTICLE

Incidence and Distribution of Foot-and-Mouth Disease in Asia, Africa and South America; Combining Expert Opinion, Official Disease Information and Livestock Populations to Assist Risk Assessment

K. Sumption[1], M. Rweyemamu[2,]* and W. Wint[3]

[1] Animal Health Department, Food and Agriculture Organization, Viale delle Terme di Caracalla, 00100 Rome, Italy
[2] 6 Robins Dale, Knaphill, Woking, Surrey GU21 2LQ, London, UK
[3] Environmental Research Group Oxford, Department of Zoology, South Parks Road, Oxford OX1 3PS, UK

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Correspondence:
Keith Sumption. Animal Health Department, Food and Agriculture Organization, Viale delle Terme di Caracalla, 00100 Rome, Italy.
Tel.: 0039 06 57055528; Fax: 0039 06 57055749; E-mail: keith.sumption@fao.org

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Summary

Risk assessment procedures frequently require quantitative data on the prevalence of the disease in question. Although most countries are members of the World Organization for Animal Health (OIE), the importance attached to foot-and-mouth disease (FMD) reporting or surveillance for infection varies enormously between infected countries. There is a general consensus that FMD outbreaks in endemic countries are greatly under-reported, to a degree related either to the economic or the political development level of the country. This exploratory study was first undertaken by FAO, but thereafter extended and reviewed by the working group on FMD risk co-ordinated by the European Food Safety Authority (EFSA). The paper attempts to overcome the lack of reporting through using expert opinion to extrapolate incidence indices from countries considered to have 'representative' levels of FMD. These were combined with livestock density distributions to provide maps of prevalence indices, which were found to be highest in China (pigs), India (cattle), the Near East (small ruminants) and the Sahel (small ruminants and cattle). Similar patterns were found when weighted expert rankings of a range of additional ranked disease parameters were also produced, and then combined with susceptible animal densities to produce a weighted multi-species density. Results suggest that the methods can provide useful information at both national and sub-national resolution, even for countries for which quantitative FMD data is currently unavailable: two of the regions identified provide little or no data on a regular basis to the OIE and therefore may be overlooked if the level of officially reported FMD is only used. As the estimated prevalences are based on recent disease history and expert opinion, they are most likely to be inaccurate where FMD incursions are infrequent as a result of the preventive measures and geographical and trade isolation. This study, therefore, highlights the need for specific detailed country risk assessments where livestock trade is under consideration. Validating the approach including ground truthing, will require collaboration between a number of agencies and institutions, in critical countries, particularly those with high disease burdens that share borders or trade livestock with currently FMD-free nations.

Introduction

The work reported here was initiated in response to a call from the FAO European Commission for the Control of Foot-and-Mouth Disease (EUFMD Commission, 35th Session, 2003) to improve the identification of FMD risk regions in Africa and Asia. To this end the EUFMD commissioned an exploratory study to identify and evaluate possible methods of providing such maps of the estimated global FMD prevalence, based on extrapolating quantitative data from indicator countries to other countries and areas which were considered epidemiologically similar, on the basis of expert opinion (Wint, 2005; http://www.fao.org/ag/againfo/commissions/en/documents/sess36/sess36/App02.pdf). The approach was also modified by ranking of FMD-related factors defined by expert opinion and based on data from the World Organization for Animal Health (OIE, 2006) and elsewhere. The methodology was further refined for the purposes of risk assessment during a study by the European Food Safety Authority on the risk assessment of FMD entering Europe from beyond its borders (EFSA 2006).

To assess the risk of FMD virus (FMDV) entering a pathway that could lead to eventual release in the European Union (EU), the authors were requested to provide quantitative information on FMD prevalence for susceptible species, on a global basis. Most analyses of the international occurrence of FMD have been limited by the quantity and quality of data reported to the OIE. A number of countries with known endemic FMD status and substantial animal populations provide no information on FMD outbreaks or provide data that is considered to be a significant under-reporting of the true situation. Further, systematic surveys for definition of prevalence of FMD are rarely conducted, and the insufficient data exists to propose multipliers to correct for disparity between prevalence based on outbreak report data and animal level prevalence based on serological detection of recovered animals.

As a result, a standardized and quantitative indication of FMD prevalence outside Europe's borders was required to provide assessors with sufficient data, broken down by livestock species likely to enter into international legal and illegal trade routes, to assess risk of entry into Europe. In addition, the estimation of the burden of infection in the endemic regions would provide a logical base on which to develop strategies to reduce the risk of FMD spread to other regions.

Species of interest were defined as: bovine animals, swine and wild boar, sheep, goats, various wild animal species (including e.g. impala), and alpaca/llama/camels. Many of the countries considered, however, either did not systematically include a column for camelids and wild fauna in their reports to OIE, or reported no cases in the study period. Purposive selection of countries where cases have been reported in these species may have allowed an estimate for those countries, but would have introduced further sources of bias. These analyses have, therefore, been limited to bovines, ovine/caprines, pigs and domesticated buffaloes.

Methods

Four distinct stages of analysis were undertaken: (a) categorizing countries according to FMD occurrence, (b) estimating incidence for each species for each defined category; (c) incorporating other indicators of FMD risk and (d) combining the incidence and other indicators with animal distributions to produce prevalence indices maps.

Country incidence categorization

Expert opinion was used to first develop a framework for country categorization, which included a category of 'conjectured incidence' (Table 1), initially with five categories (1–5) of conjectured incidence, later extended to subcategories, ranging from officially recognized as FMD free (category 1) to a high incidence with outbreaks throughout the year (category 5). An expert panel then assigned each country to one of these categories.

The validity and comparability of these incidence categories was assessed by comparison with the reported incidence of FMD in randomly selected countries within categories 2–5, i.e. those where FMD is expected at least once every 5 years. The incidences used for validations were calculated using the number of FMD cases in each

Table 1. Criteria for (conjectured) FMD Country Profile

	CONJFMD category
Country information not available/entered	−1
Whole country classified by OIE as FMD free	1
Low sporadic incidence with effective reporting (one to three episodes in 5 years)	2
Apparently low sporadic incidence with ineffective reporting (one to three episodes in 5 years)	3
Disease expected every year (seasonal and/or restricted)	4
If involving pigs with the Cathay topotype of type O (pig-adapted type)	41
If involving only SAT virus types	42
High incidence with outbreaks throughout the year	5
If involving pigs with the Cathay topotype of type O (pig-adapted type)	51
If involving only SAT virus types	52

species in the most recent 5-year period (1999–2003), as reported in the annual country reports to the OIE; countries with <3 annual reports in this period were excluded from the analysis. Denominator data was the population at risk, as reported by countries to FAO (FAOSTAT database; FAO, 2006).

Analysis of the incidence data supported the categorization of conjectured incidence. However, the exceptionally high incidence in pigs in Hong Kong SAR, and the very low incidence of FMD in small ruminants and pigs in southern Africa, was considered the probable result of the presence of a pig-adapted strains of type O in Hong Kong, and bovine-associated SAT viruses in southern Africa. Therefore, the expert panel proposed an additional subdivision of categories 4 and 5, with countries reclassified based on known distribution of pig adapted 'Cathay' type O viruses and of SAT types (Table 2).

Estimating annual incidence for species and country category

The values used for initial category validation were used as a basis for estimates of FMD incidence by species, for each category of conjectured incidence, as shown in

Table 2. Classification of territories categorized as level 2 or higher

CJFMD 2	CJFMD 3	CJFMD 4	CJFMD 41,42	CJFMD 5		CJFMD 51,52
Algeria	Armenia	Bolivia[a]	Macau (41)	Afghanistan	Kyrgyzstan	China (51)
Argentina[b]	Azerbaijan	Colombia[c]	Malawi (42)	Angola	Laos	Vietnam (51)
Bahrain	Comoros[d]	Ecuador		Bangladesh	Liberia	Mozambique (52)
Botswana	Egypt	Gaza Strip		Benin	Mali	
Brazil[e]	North Korea (DPRK)[g]	Kazakhstan		Bhutan	Mauritania	
Cape Verde	Paraguay	Lebanon		Burkina Faso	Myanmar (Burma)	
Georgia	Peru	Mongolia		Burundi	Nepal	
Israel	Qatar	Saudi Arabia		Cambodia	Niger	
Jordan	Sao Tome and Principe	Tajikistan		Cameroon	Nigeria	
Libya	Uzbekistan	Turkey		Central African Republic	Oman	
Malaysia	Zambia	Venezuela		Chad	Pakistan	
Morocco		West Bank		Congo	Rwanda	
Namibia				Djibouti	Senegal	
Philippines[f]				Equatorial Guinea	Sierra Leone	
Russia				Eritrea	Somalia	
South Africa				Ethiopia	Sri Lanka	
Taiwan				Gabon	Sudan	
Tunisia				The Gambia	Syria	
United Arab Emirates				Ghana	United Republic of Tanzania	
Uruguay				Guinea	Thailand	
Western Sahara				Guinea-Bissau	Togo	
				India	Turkmenistan	
				Iran	Uganda	
				Iraq	Yemen	
				IvoryCoast	Zaire	
				Kenya	Zimbabwe	
				Kuwait		

The Table was compiled in early 2005 and has not been updated with subsequent country and zonal freedom changes recognized by the OIE (for current position, refer to http://www.oie.int).

[a]In Bolivia level 4 was applied as FMD is considered endemic (regular occurrence throughout the year) but in restricted zones; other zones (Santa Cruz) had OIE status of DF with vaccination.

[b]Argentina has zones which are FMD free without vaccination, and zones FMD free with vaccination. The conjectured FMD level 2 was applied since in the 5-year period under consideration several incursions had occurred in the zone where vaccination is applied.

[c]Colombia has an area mainly in the south where FMD is continues to persist, therefore level 4 (FMD in a restricted area) was applied. The country also has OIE recognized DF zones.

[d]For Comoros, on the precautionary principle, level 3 was applied given that the country's frequency or detail in reporting to the OIE had been very unsatisfactory in the past 5 years.

[e]Brazil had OIE recognized disease FMD-free states in which a high proportion of national cattle were located. FMD was restricted to Amazon basin states.

[f]In the Philippines level 2 was applied as the reported occurrence is geographically restricted, even though at the time of compilation reports indicated that infection occurs every year in the affected zone.

[g]For South Korea level 1 was applied as two recent incursions had been rapidly controlled, the last without vaccination applied.

Tables 3 and 4. For categories 2–4, the mean annual incidence in each category was selected and these levels assigned to countries in these categories (Table 5). To reduce the level of the underestimate in the countries where under-reporting is most expected (i.e. category 5), and where incentives to report to the authorities are limited, it was assumed that the incidence would be similar to that observed at the higher end of the range for category 5 countries. These 'high end' incidences were then applied to other countries which are considered to have, through expert opinion, a similar conjectured level of FMD and have putatively similar epidemiological situations in terms of virus types present.

Where, however, pig-adapted viruses were known to be present, or only SAT viruses, several assumptions had to be made, as indicated in the footnotes of Table 5. For categories 41 and 51, estimates were based on the data for Hong Kong SAR. In the absence of sufficient data for endemic countries affected by only SAT viruses, the cattle incidences was assumed to be similar to that of Iran, but the small ruminant incidence assumed to be 20% of the Iran incidence, based on the limited reported incidence of SAT viruses from small ruminants during epidemics. Given that cattle are the usual indicator of FMD presence, under-reporting is probably least for bovines compared with other species. From this, it was assumed that the more disease is present in cattle the more the disease will be present in other species, and estimated incidence was calculated pro rata, where reported incidences were considered unreliable. This assumption may not be expected to hold in the case of virus types adapted to particular hosts.

Table 3. Incidence (per 1000 animals/year) by species in selected countries in conjectured incidence categories 2–5 using population and OIE report data for estimation

Country	Years of data	Incidence/1000 animals/year: Cattle	Pigs	Ovine/caprine	Dom. buffalo
Level 2					
Tunisia	5	0.00605	0.00000	0.00019	0.00000
Namibia	5	0.00048	0.00000	0.00000	0.00000
Botswana	5	0.01106	0.00000	0.00000	0.00000
Israel	5	0.17436	0.00000	0.22183	0.00000
Level 3					
Egypt	5	0.00031	0.00000	0.00005	0.00000
Zambia	4	0.08769	0.00000	0.00000	0.00000
Qatar	5	4.50667	0.00000	1.59737	0.00000
Level 4					
Kazakhstan	4	0.02533	0.00000	0.00073	0.00000
Tajikistan	5	1.24969	0.00000	0.13161	0.00000
Malawi	5	1.95173	0.00000	0.00342	0.00000
Mongolia	4	0.31000	0.00000	0.00100	0.00000
Level 5					
Kuwait	5	4.46000	0.00000	2.44898	0.00000
Zimbabwe	5	1.24587	0.00000	0.00000	0.00000
Congo Dem	4	0.20800	0.00000	0.00000	0.00000
China[a]	1	0.00013	0.0026	0.00000	0.00000
India	5	0.29	0.0076	0.02	0.05
Iran	5	3.39	0.00000	1.72	0.00536
Burkina	5	1.56	0.0296	0.00000	0.00000
Uganda	4	1.4	0.00000	0.00000	0.00000
Senegal	4	0.05	0.00000	0.00000	0.00000
Thailand	4	2.20451	0.16822	0.00000	0.39083
Hong Kong SAR	5	0.00000	24.5600	0.00000	0.00000

[a]China was included in the randomly selected category 5 countries but as FMD data had been submitted for 1 of 5 years, Hong Kong SAR was selected as a proxy.

Other indicators of FMD risk

Whilst disease incidence is undoubtedly a key indicator of risk, there are likely to be a number of other factors that affect the probability of FMD outbreaks – or the movement of the disease from one country to another. In attempt to quantify these additional influences, expert opinion was used to rank countries according to a series or criteria set out in Table 6, including disease reporting inefficiency to the OIE (based on the level of completeness of monthly FMD reports over a 5-year period), presence of wildlife hosts capable of acting as carriers (Africa only), effectiveness expected in control over movement across country borders (expert opinion), official (OIE) FMD status at time of the study, and the number of FMD serotypes observed in a 10-year period (from the World Reference Laboratory for FMD reports to FAO). Higher levels in the scoring were considered likely to contribute to an increased frequency of new disease events.

In the absence of an objective weighting system, conjectured FMD subcategories were recoded to the parent values, the unweighted ranks of the additional criteria were then simply summed, and the proportion of the maximum possible score calculated – thereby allowing for missing values (as the presence of wildlife was considered a risk factor in Africa but not scored for other regions) – to produce a normalized FMD Country Profile Score.

Combination of country profiling with incidence to produce a density-weighted global FMD distribution map

To provide some indication of the numbers and distributions of animals affected by FMD, the two sets of risk indicators – incidence index and profile score – were each combined with animal distributions. First, an indication of the distribution of the total burden of FMD within countries was made by combining the incidence index with the global distribution of each livestock species to

Table 4. Mean and median incidence values/1000 animals/year in randomly selected countries in categories 2–5

CONJFMD level	No. countries	Estimate	Cattle	Pigs	Ovine/caprine	Domestic buffalo
2 and 3	6[a]	Mean	0.04666	0.00000	0.03701	0.00000
		Median	0.00856	0.00000	0.00002	0.00000
4	4	Mean	0.88419	0.00000	0.03419	0.00000
		Median	0.77985	0.00000	0.00221	0.00000
5	11	Mean	1.34623	2.25164	0.38082	0.04056
		Median	1.32293	0.00130	0.00000	0.00000
	9[b]	Mean	1.64538	0.02282	0.4654	0.04958

[a]Excludes Qatar as the incidence in cattle and small ruminants was observed to be similar to category 5 countries.
[b]Excludes China and Hong Kong SAR.

Table 5. Estimated incidence, as CJFMD categories, per 1000 animals per year, by species and category of country

		Estimated incidence rate (/1000 animals/year)			
Categorization criteria	Level	Cattle	Pigs	Sheep & goats	Buffalo
Whole country FMD free	1	0	0	0	0
Low sporadic incidence with effective reporting	2	0.047[a]	0.002[b]	0.037[b]	0.0054[b]
Apparently low sporadic incidence, ineffective reporting	3	0.047[a]	0.002[b]	0.037[b]	0.0054[b]
Disease expected every year (seasonal and/or restricted)	4	0.884[c]	0.044[d]	0.445[e]	0.1[f]
High incidence with outbreaks throughout the year	5	3.388[i]	0.168[j]	1.720[k]	0.391[l]
As 4, but involving Cathay topotype of type O in pigs	41	0.884[g]	6.408[h]	0.445[b]	0.1[b]
As 4, but involving only SAT virus types	42	0.884[q]	0.044[q]	0.090[r]	0.12[f]
As 5, but involving Cathay topotype of type O in pigs	51	3.388[i]	24.560[m]	1.720[c]	0.391[c]
As 5 but involving only SAT virus types	52	3.388[i]	0.168[n]	0.344[o]	0[p]

[a]Mean incidence for six countries in categories 2 and 3, this study.
[b]Pro rata calculation, using relative cattle incidences (Cat 42/Cat 5), multiplied by species incidence in Cat 5.
[c]Mean incidence for four countries in category 4, this study.
[d]The studied countries could not be considered to provide an indicator for countries with high pig populations and husbandry systems that would support spread. Also see note h about pig-adapted viruses.
[e]The mean incidence in small ruminants in the four countries studied was not considered reliable. The figure proposed is proportional to cattle incidence, using surveillance data from Iran as indicative of infection in small compared with large ruminants, and assuming that category 4 countries have reduced number of outbreaks in ruminants, but with similar species involvement to category 5.
[f]As in note 5, buffalo incidence is assumed proportional to cattle incidence, using estimators from category 5 countries.
[g]In countries where mixed types expected including the Cathay topotype of type O, a higher incidence in pigs is estimated. Cattle incidence assumed as per category 4 may be overestimated where only Cathay type present.
[h]The estimate uses Hong Kong incidence, using relative estimates of cattle incidence of categories 4 and 5.
[i]The incidence level in cattle observed over 5-year period in Iran, a country with a well-resourced national surveillance programme, is used. The figure is not the highest in the category (Kuwait, 4.46/1000 head).
[j]The two estimates for countries in Southeast Asia differed widely, from 0.168 (Thailand) to 24.56 per 1000 pigs (Hong Kong SAR). The factors that account for this are unclear. The higher estimate may relate to species adaptation (Cathay type), in which case the higher estimate may be applied to pig populations in countries where this is considered present, and the lower estimate to others.
[k]The incidence level in cattle observed over 5-year period in Iran, a country with a well-resourced national surveillance programme, is proposed for these countries. The figure is not the highest in the category (Kuwait, 2.44/1000 head). It is assumed that the low levels reported from other non-FMD-free countries with similar husbandry features represent significant under reporting.
[l]The incidence level from Thailand is proposed, a country with a relatively well-resourced surveillance system. Only two countries were considered, Thailand and India.
[m]Hong Kong rate, to be applied to countries where mixed topotypes including Cathay type are present.
[n]Assumes lower pig incidence rate of Thailand.
[o]Data not available. Assumption of 20% of species incidence in Cat 5.
[p]Refers to domesticated buffalo which are assumed not present/involved.
[q]Data limited. Value applied is the (default) incidence level for species in a Cat 4 country.
[r]Pro rata calculation, based on relative cattle incidences (Cat 42/Cat 52), multiplied by species incidence in Cat 52.

Table 6. Criteria for ranks used in FMD country profiling

Column or rank definition	Rank
Official FMD Status (OIE)	Oiestat
Country information not given by OIE	−1
Country free without vaccination	1
Country free with vaccination	2
Country contains zone free without vaccination	3
Country contains zone free with vaccination	4
OIE unrecognized FMD status	5
Epidemiological characteristics	Epitype
Note of presence of FMD viruses which may lead to higher or lower incidences in particular domestic species	
Conjectured FMD incidence	CONJFMD
Country information not available/entered. For details of other ranks see Table 1	−1, 1–5
Presumed number of serotypes (10-year aggregate)	
None or eliminated from livestock	1
One to seven serotypes	2–8
Wildlife species (Africa only)	
None or confined to designated and segregated areas; no infected carrier species	1
Free-roaming but no infected carrier species	2
Confined to designated and segregated areas but include potentially infected carrier species	3
Free-roaming including potential carriers; occasional contact with grazing livestock	4
Free-roaming including potential carrier animals; no restriction on contact with livestock	5
Reporting (to OIE) efficiency	
Likely most outbreaks detected and reported	1
Moderate under-reporting; reliance on passive reporting	3
Likely to be severe under-reporting of disease/infection in significant livestock population at risk	5
Border control	
Effective land border security	1
Default	3
No effective border security	5
Conjectured export/cross-border movement	
Export/movement limited to neighbour	1
Export/movement beyond neighbour (limited)	2
Export/movement beyond neighbour (extensive)	3
Export to West Asia and/or North Africa (WANA)	4
Export to Europe	5

produce a species-specific prevalence index. Animal distributions were derived from the FAO Gridded Livestock of The World datasets (FAO, 2007), which provides 5 km resolution density maps of each of the major livestock species.

Second, a multi-species density weighted FMD distribution was produced by combining the normalized FMD Country Profile Scores with the animal distributions. As the Country Profile Scores are not species specific, the livestock distributions were summed into a single figure for numbers of susceptible animals per square kilometre. This is distinct from the more usual biomass maps, (where animal numbers are combined according to their bodyweights), because disease risk does not depend on bodyweight. The calculated value is, therefore, simply the summed animal density multiplied by the normalized Country Profile Score.

Results

The categorization of countries with a incidence level >1 (i.e. where FMD outbreaks occur at least once every 5 years) is shown in Table 2 and illustrated in Fig. 1. Countries whose status was discussed on a case-by–case basis and where a footnote was considered necessary to provide additional information on the selection of a particular level are detailed in 'Notes' below the table.

The calculated Prevalence Index maps provide an indication of the sub-national distribution of the species-specific burden of disease within countries. The results are presented for cattle, small ruminants, and pigs in Figs 2–4 respectively. Estimated disease burden is highest in China (pigs), India (cattle), the Near East (small ruminants) and the Sahel (small ruminants and cattle).

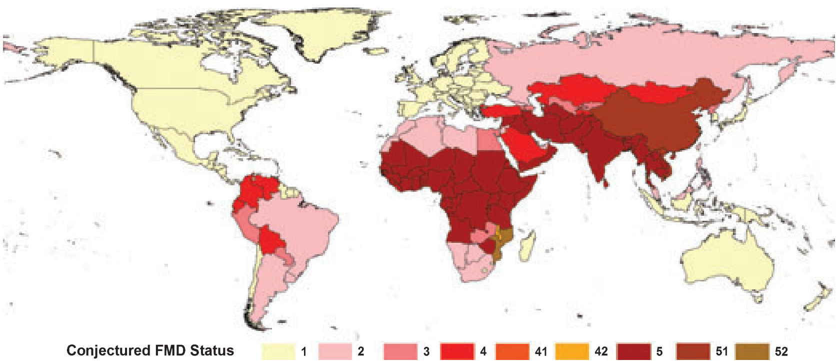

Fig. 1. Conjectured FMD status (details in Table 2).

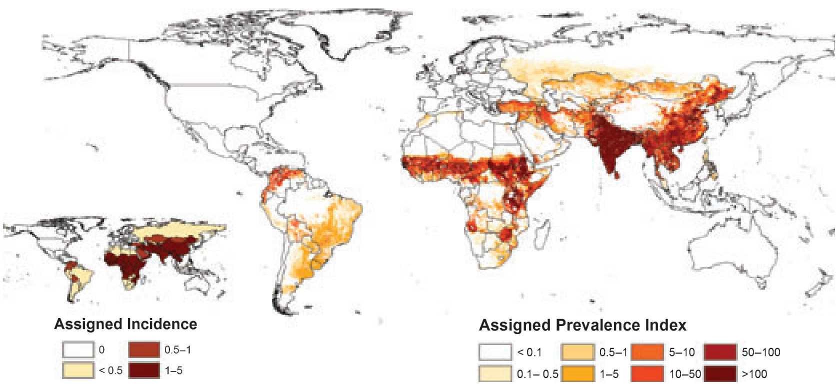

Fig. 2. Assigned incidence and prevalence indices: cattle.

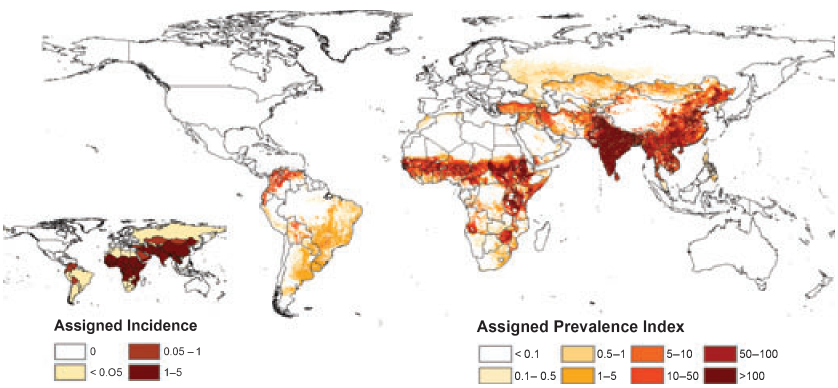

Fig. 3. Assigned incidence and prevalence indices: small ruminants.

The normalized Country Profile Score summarizing the additional FMD-risk parameters is shown in Fig. 5. The multi-species density weighted FMD distribution, derived using the Profile Score together with animal density distributions, is shown in Fig. 6. This suggests the pattern of potential multi-species disease burden is greatest in China (pigs), India (cattle), the Near East (small ruminants) and the Sahel (small ruminants and cattle). This is not dissimilar to the patterns suggested by the assigned incidence analysis presented above, which suggests that both approaches have some merit.

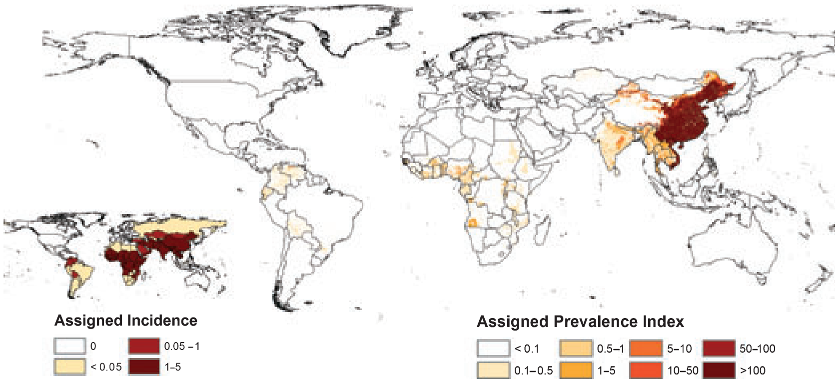

Fig. 4. Assigned incidence and prevalence indices: pigs.

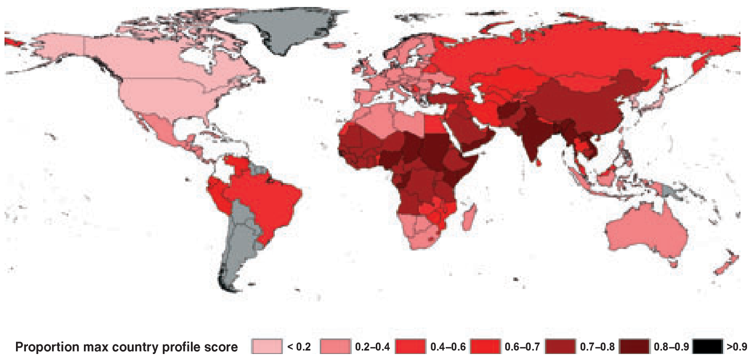

Fig. 5. Proportion of maximum total FMD Country Profile Score.

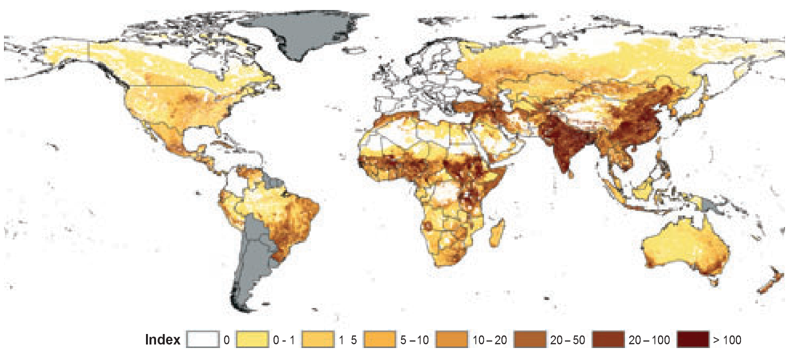

Fig. 6. Multi-species weighted FMD distribution indication, derived from the normalized Country Profile Score times total animal density. The scale represents a susceptible population weighted index, incorporating the country profiles, and therefore reflects expert opinion at the time of the study, and should not be considered an official view of actual FMD status. Since large countries are not subdivided according to proximity to infected neighbours, it does not reflect variation in risk within countries. Countries that were officially completely free of the disease (category 1) have been excluded (assigned a value of zero).

Discussion and conclusions

In the approaches used the main variable driving the number of cases is the population at risk, and thus the importance of countries will depend on their relative populations. Although this may under-estimate particular high- or low-risk husbandry situations, it avoids the under-representation of some endemic countries with large livestock populations. It is accepted that focussing on the application of annualized incidence rates may mask particular risks, such as associated with virus types where the level of antigenic divergence is such that on a unit basis they present a higher risk of breaking through the local vaccination programmes, and possibly the emergency banks kept in the EU. More systematic study may reveal patterns of virus persistence and emergence that would enable refinement of the risk assessment, as in some regions, notably in South America, FMD persistence (endemicity) is most associated with low-density cattle operations ('primary endemic areas') and not highly dense populations. At some critical point, where contact rate of animals is too low, virus cannot continue to circulate as acute infections and thus more sophisticated approaches are needed to address density and vaccination impacts upon prevalence. Further data analysis should also lead to refinement of the rates estimated in this preliminary study, and the inclusion of stochasticity in estimates as can be expected for an infection which circulates within endemic regions in waves. The data and expert opinion underlying the analyses must also be validated and if possible extended specifically by validating assigned incidence levels in critical countries, particularly those with high disease burdens that share borders or trade livestock with currently FMD-free nations; and evaluating key indicators, such as sero-conversion rates in selected age groups. Work is also required to better refine the approach, using validation with serological and other methods to estimate prevalence in indicator endemic countries. This should be possible through systematic use of the opportunities from field surveillance actions to collect reference data to validate this and other approaches.

Results suggest, however, that the exploratory methods presented here can be used to provide a useful baseline of information at national and sub-national resolution, for countries for which quantitative FMD data is currently unavailable. These baseline disease distributions need to be validated at least by national expert panels, using a variety of information in addition to officially reported data. The techniques assessed can also be significantly improved by making the rankings more robust by introducing additional parameters and evaluating alternative weighting regimes to compensate for variation within conjectured FMD categories.

It is accepted that circulation of rinderpest virus occurred in ecosystems that were defined by the frequency of contact of animal groups within, rather than between, these ecosystems (Rweyemamu, 1999). Molecular data on FMD epidemiology also supports the circulation of virus in ecosystems, as virus relatedness appears usually much higher within a geographical region. It is noteworthy that the high-density 'clusters' observed in Fig. 6 correspond approximately to the ecosystems observed from molecular typing, for example the Eurasian (Iran/Turkey/Iraq), south Asian (India/Bangladesh/Nepal), far-east (China/Vietnam), west and east African ecosystems. Given that FMD viruses have been observed to jump between these ecosystems (Knowles and Samuel, 2003), reflecting patterns of animal and product movement between continents, there would appear no rigid segregation of virus ecosystems, although south America may be the exception as new incursions into that region from outside of the hemisphere have not been observed.

Combining animal distribution with molecular genotyping should assist to elucidate these ecosystems in FMD. In particular using more sophisticated spatial analysis tools, such as watershed analysis, classification and segmentation and iterative spread modelling should help identify 'self contained' disease systems and define limits to likely circulation and spread of 'waves' of infection.

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