Global trends in infectious diseases of swine

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Pork accounts for more than one-third of meat produced worldwide and is an important component of global food security, agricultural economies, and trade. Infectious diseases are among the primary constraints to swine production, and the globalization of the swine industry has contributed to the emergence and spread of pathogens. Despite the importance of infectious diseases to animal health and the stability and productivity of the global swine industry, pathogens of swine have never been reviewed at a global scale. Here, we build a holistic global picture of research on swine pathogens to enhance preparedness and understand patterns of emergence and spread. By conducting a scoping review of more than 57,000 publications across 50 years, we identify priority pathogens globally and regionally, and characterize geographic and temporal trends in research priorities. Of the 40 identified pathogens, publication rates for eight pathogens increased faster than overall trends, suggesting that these pathogens may be emerging or constitute an increasing threat. We also compared regional patterns of pathogen prioritization in the context of policy differences, history of outbreaks, and differing swine health challenges faced in regions where swine production has become more industrialized. We documented a general increasing trend in importance of zoonotic pathogens and show that structural changes in the industry related to intensive swine production shift pathogen prioritization. Multinational collaboration networks were strongly shaped by region, colonial ties, and pig trade networks. This review represents the most comprehensive overview of research on swine infectious diseases to date.

livestock | infectious diseases | global health | agricultural practices | emerging pathogens

Agriculture contributes more than $3 trillion USD to the global economy and comprises up to 15% of gross domestic product for high income countries and an average of 30% for low income countries (1). With human populations rapidly growing worldwide, food security will be an increasing concern over the coming decades. Demand for animal-based protein is also expected to expand with a growing middle class. Pork production, which accounts for more than one-fourth of total protein consumed worldwide (2), has increased over the past several decades and now accounts for ∼35% of all meat production (3). The demand for pork has led to intensification of production, with farms often housing thousands of animals in densities conducive to rapid pathogen transmission (4). Infectious diseases result in direct losses to livestock production through mortality, loss of productivity, trade restrictions, reduced market value, and often food insecurity (5). The constant threat of endemic and emerging diseases affecting swine, which in some instances also impact human health, highlight the potential vulnerability of pork production around the world. Indeed, infectious diseases of swine are among the primary constraints to pork production and trade (6).

The intensification and globalization of the swine industry has contributed to the emergence and global spread of pathogens of swine, driven in part by frequent movements of pigs, feed, and pork products at local, national, and international scales (7). For example, porcine epidemic diarrhea virus (PED) spread from China to the United States in 2013, and within 1 y, the virus had impacted ∼50% of US breeding herds, resulting in the deaths of at least seven million piglets (8). African swine fever (ASF) emerged in Eastern Europe from sub-Saharan Africa in 2007 and currently is causing high mortality outbreaks and restricting international trade throughout the region. The risk of the virus spreading to countries currently not affected is significant (9), as shown by its recent 2018 introduction to China, the world's largest producer of pigs (10). Finally, the potential importance of livestock pathogens for human public health was exemplified by the H1N1 "swine flu" pandemic in 2009, which originated from influenza A viruses circulating in pig populations (11). These examples highlight the need to build a holistic global picture of pathogens of swine to enhance preparedness and understand patterns of emergence and spread.

Despite the importance of infectious diseases to animal health and the stability and productivity of the global swine industry, infectious diseases of swine have never been reviewed at a global scale. Here, we evaluate publication trends on swine pathogens under the assumption that publication trends capture varying and evolving research priorities. We assume that published research can be used as an indicator of research priorities and the availability of funding within a country; funding sources (industry or governmental) play a role in shaping research and will tend to focus research efforts toward endemic or foreign pathogens with higher prevalence, health consequences, or economic impact. Publication trends should not be taken as an indicator of the occurrence of clinical disease, but rather as an indicator of the prioritization of a given pathogen (e.g., foreign animal diseases or foodborne pathogens that may or may not cause clinical disease in pigs). Here, we conduct a scoping literature review (12) of global and regional trends in swine pathogen research. Our objective is to identify priority swine pathogens, characterize temporal and geographic trends in research priorities, and evaluate factors that shape international research collaboration networks.

Significance

Pig production is an important component of global food security, agricultural economies, and local and international trade. Infectious diseases impact pig health and the stability and productivity of the global swine industry. By reviewing >57,000 publications on swine diseases, we identify priority pathogens in different regions and document shifting research priorities across 50 years. Publication rates for some pathogens have accelerated in recent years, highlighting the emerging or increasing threat of these pathogens to human and swine health. Our findings provide a global overview of research on swine pathogens, which can be used to make better decisions and policies that reduce the vulnerability of global swine industry.

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Table 1. **Overall publication counts (1966–2016) for swine pathogens**

Pathogen	Count	Type	Pathogen	Count	Type
1. *Salmonella* spp.	6,466	*Z, P*	21. *S. hyodysenteriae*	1,143	*P*
2. *E. coli*	4,985	*Z, P*	22. *Campylobacter* spp. [Latin America]	974	*Z*
3. Influenza	4,729	*Z, P*	23. Porcine parvovirus	952	*P*
4. Pseudorabies (Aujeszky's disease)	4,170	*R*	24. Japanese encephalitis virus [Australia/New Zealand; South/SE Asia]	941	*Z*
5. FMD	3,867	*R*	25. *Mycobacteria* spp. [Africa]	882	*Z*
6. PRRS	3,683	*P*	26. Rotavirus [South/SE Asia]	868	*P*
7. Classical swine fever	3,113	*R*	27. *Haemophilus parasuis*	791	*P*
8. APP	2,552	*P*	28. *Brucella* [Australia/New Zealand; West/Central Asia; Latin America]	784	*Z*
9. *Trichinella* spp. [South America/Eastern Europe]	2,327	*Z*	29. *Leptospira* [Latin America]	763	*Z*
10. ASF	2,246	*R*	30. *Erysipelothrix rhusiopathiae* [Australia/New Zealand]	684	*P*
11. *P. multocida*	2,099	*P*	31. PED	684	*P*
12. Porcine circovirus type 2	1,947	*P*	32. Vesicular stomatitis virus	640	*R*
13. *A. suum*	1,941	*P*	33. *L. intracellularis*	554	*P*
14. Transmissible gastroenteritis virus	1,817	*P*	34. *T. suis* [Africa; West and Central Asia]	516	*Z*
15. *Staphylococcus aureus*	1,812	*Z*	35. *Trypanosoma* spp. [Africa]	403	*Z*
16. *S. suis*	1,776	*Z*	36. *Echinococcus* spp. [Africa]	401	*Z*
17. *Mycoplasma hyopneumoniae*	1,665	*P*	37. Nipah virus [South/SE Asia]	398	*Z, R*
18. *T. solium*	1,369	*Z*	38. *Fasciolopsis buski* [Southern Asia]	72	*Z*
19. *T. gondii*	1,344	*Z*	39. *Metastrongylus salmi* [West and Central Asia]	58	*P*
20. Hepatitis E virus	1,330	*Z*	40. Menangle virus [Australia/New Zealand]	39	*Z*

Letters indicate zoonotic pathogens (Z), diseases affecting production (P), and reportable diseases (R). Bracketed region names indicate pathogens that were included in the top 40 because of high publication counts in specific regions. Numbers listed here exceed the total publication count because some publications included multiple pathogens.

Results and Discussion

Overall, 57,471 publications from 1966 to 2016 were included in this analysis (Table 1). This database was assembled from literature searches on 40 swine pathogens [PubMed, Web of Science (Centre for Agriculture and Biosciences International), and Scopus]. These pathogens were selected as the most published infectious agents of swine globally or regionally using computer-assisted annotation of bioconcepts (i.e., organisms and diseases) found in PubMed abstracts (13). The top-40 pathogens included 16 viruses, 15 bacteria, 8 helminth parasites, and 1 protozoan (Table 1). The most published viruses included influenza, pseudorabies (Aujeszky's disease), foot and mouth disease (FMD), and porcine reproductive and respiratory syndrome (PRRS). The most published bacteria included *Salmonella*, *Escherichia coli*, *Actinobacillus pleuropneumonia* (APP), and *Pasteurella multocida*. For helminths, the most important parasites were *Trichinella* and *Ascaris suum*. In general, there were fewer publications on protozoa and helminths than bacteria and viruses, particularly in recent years as better control was achieved with the introduction of avermectins and improved biosecurity.

All pathogens could be classified into three categories: reportable diseases, pathogens listed as notifiable disease by the World Organization for Animal Health; production diseases, not reportable, but have negative impacts on mortality, morbidity, reproduction, or growth; and zoonotic diseases, interest in pathogen is primarily motivated by impacts on human public health. Six pathogens in the top 40 were reportable, four of which were in the top 10 overall (Table 1). Nineteen pathogens were considered production diseases, although several of these also were zoonotic (e.g., *Salmonella* spp., *E. coli*). Based on research effort, other important production diseases globally include PRRS and APP. Twenty pathogens were zoonotic, although several of these can also be considered production diseases. The top three pathogens in terms of publication counts were all zoonotic, which likely reflects the increased funding availability and larger research community engaged in human health research compared with swine research. Many organisms in Table 1 are highly diverse with substantial strain- level or lineage-level variation in pathogenicity. Influenza, for example, can be both a public health and animal productivity concern depending on strain. Viral evolution and reassortment of influenza within pig populations is still poorly understood and poses a challenge for control. While evaluating temporal trends in different lineages of a pathogen would provide additional value, it was not possible to extract strain-level or lineage-level detail using available tools for bioconcept annotation.

To assess regional research priorities over the past 10 y, we also identified the top-five pathogens by region according to publication counts (Fig. 1 and *SI Appendix*, Table S1). Influenza was ranked as first or second in all regions except sub-Saharan Africa, where it was fourth. Thus, it was excluded from Fig. 1 so that pathogens that varied by region could be better compared. It is important to note that a pathogen tends to be prioritized not only in areas where it is endemic, but also in areas where large epidemics have or could occur. FMD, for example, is ranked in the top five in most regions where it is endemic (e.g., Africa and parts of Asia), but also in areas that have experienced past outbreaks (such as the United Kingdom in Northern Europe) or where the disease does not occur but FMD prevention and preparedness are prioritized (such as Australia).

Regional differences are also apparent between developed (more temperate) and developing (more tropical) regions. Helminth parasites, such as *Taenia solium* and *Toxoplasma gondii*, appear far more frequently in the top five of developing than developed regions. This likely reflects a shift in common disease challenges faced in backyard or small-holder production (more protozoa and helminths) compared with more intensified production and greater sanitation common in developed countries (more bacteria and viruses).

Compared with Northern America, European (particularly Western and Northern Europe) publications tend to center more on pathogens related to zoonotic, foodborne concerns, reflecting policy differences and priorities in Europe. During the late 1990s and early 2000s, the European Union (EU) phased in more

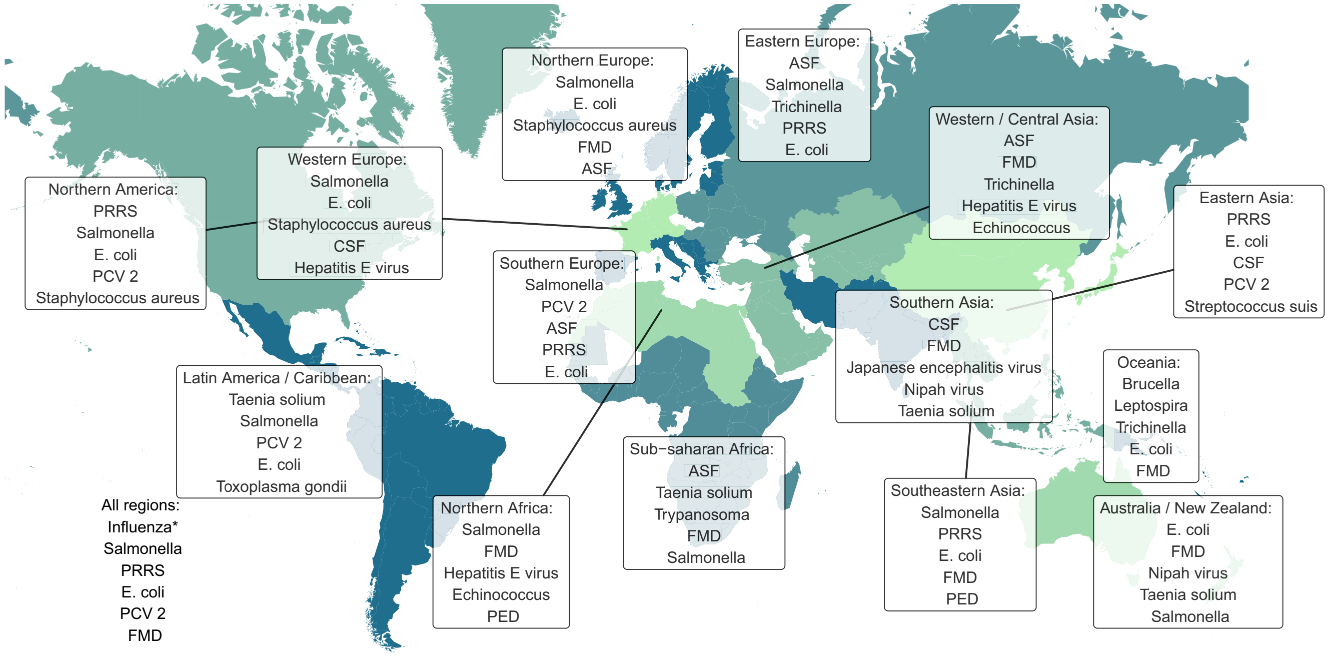

Fig. 1. Most important pathogens of swine by region during 2006–2016, ranked in descending order by publication number. Asterisk indicates pathogens appearing on each regions list and thus excluded from regional lists.

stringent regulations on the use of antimicrobial substances in production, particularly their use for growth promotion, which highlights the contrasting regulatory frameworks present in Northern America and the EU (14). Also in the early 2000s, the EU enacted policies for the on-farm surveillance and control of *Salmonella* in poultry and pigs, whereas the United States has no mandated effort to control *Salmonella* in live pigs and instead focuses on abattoir-based control methods (15). Potentially interrelated with these policies, publications on *Salmonella* account for at least 10% of publications for all European regions, and more than 15% for Northern Europe, which is starkly higher than patterns seen in Northern America. Continued debate in the scientific literature on the efficacy of on-farm practices for reducing *Salmonella* burdens may contribute to the higher relative ranking of *Salmonella* in Europe. The example of *Salmonella* highlights how differences in policy can both stimulate or be influenced by research.

Long-Term Trends. The most published pathogens of swine have shifted over the past 50 y (*SI Appendix*, Table S2). In recent decades, reportable disease appeared in the top 10 more rarely and fell in rank compared with 40–50 y ago. Research effort appears to be relatively constant on reportable diseases, with publication counts increasing proportionally to overall publication counts on all swine diseases (i.e., FMD in Fig. 2). Their fall in rank likely is reflective of overall shifting research priorities and funding availability. For example, since the 1960s and 1970s, pathogens associated with production have been steadily rising in rank (*SI Appendix*, Table S2). This greater prominence of production diseases in the swine literature may be related to growing intensification of swine production over this period (4). Intensification has been aligned with increased abilities to measure the effects of diseases upon productivity and quantify the economic benefits of their control. However, in the most recent 10 y, swine infectious agents that also have public health implications have drastically increased in ranking, probably due to an overall shift in global research priorities and funding to public health, as well as greater concerns by the swine industry about zoonotic diseases and their effect on demand.

The number of publications on swine disease has steadily increased through time (Fig. 2*A*), reflecting the generally increasing amount of research effort worldwide. Pathogen-specific long-term trends followed one of several patterns: expected, faster than expected, or slower than expected. In Fig. 2, we show several representative time series for each trend type. Publication trends for

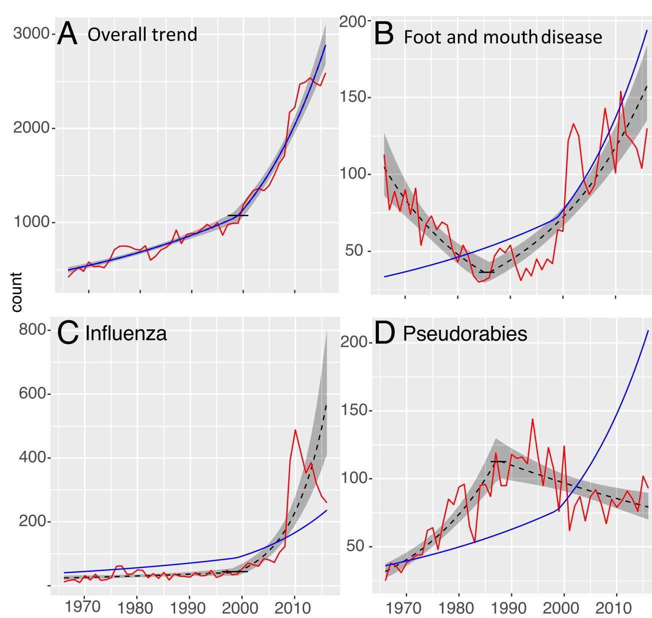

Fig. 2. Changes in publication count per year over time overall (*A*), and for FMD (*B*), influenza (*C*), and pseudorabies (*D*). Red lines represent count per year. Hashed lines and shading represent the fitted regression line (+SE) of a GLM with a negative binomial link function. A changepoint analysis was performed to estimate the year in which the slope changed and the slope before and after this changepoint. Horizontal line segments indicate the year of a slope changepoint. The blue line represents the expected trend based on overall publication counts (*A*), which was used to assess whether publication rates for specific pathogens were growing faster or slower than the general trend for swine diseases.

all pathogens are included in *SI Appendix*, Fig. S1 and Table S3. First, 20 diseases seem to follow the general expectations for rate of increase in publications (as depicted by the blue line in Fig. 2), which can be interpreted as a relatively constant interest in the pathogen across time. For example, the rate of increase in FMD publications (dotted line) follows the expectation quite closely (Fig. 2*B*). However, research on FMD appears to have waned throughout the 1970s and resurged in 2001, coinciding with both the epidemic in the United Kingdom and the post-September 11 recognition of FMD as a potential bioterrorism threat (16).

Eight pathogens increased faster than expected, particularly in the past 15 y (e.g., Fig. 2*C*). Pathogens in this group can be considered emerging and include two zoonoses (hepatitis E virus, Nipah virus), two zoonotic diseases that also affect production (influenza and *Streptococcus suis*), and four production diseases (*Lawsonia intracellularis*, porcine circovirus 2, PRRS, and PED). The rapid increase in publications associated with these diseases can be interpreted as emergence of these diseases along with heightened prioritization and associated funding available for research on these pathogens. For example, publications related to influenza in swine spiked immediately after the so-called "swine flu" epidemic in 2009 (Fig. 2*C*), likely driven by enhanced interest from the public health community in influenza circulating in swine populations (11). Similarly, publications on PED increased precipitously when the disease emerged from Eastern Asia in 2013 (8), causing large epidemics in North America and elsewhere. When PED publication trends are broken down by region, it is apparent that increases in PED publication rates increased in Eastern Asia approximately 2 y before the epidemic in North America in 2013 (Fig. 3*A*).

Twelve pathogens increased slower than expected, suggesting that research effort on these pathogens has decreased over time. Seven showed a relatively flat trend in the number of publications per year. Of these seven, five were pathogens only included in our study due to being of regional importance and, thus, may not be a particular research priority worldwide. The remaining two, *A. suum* and *Trichuris suis*, are helminth parasites, and decreasing interest in these parasites may reflect their diminished presence in more intensive swine production.

The remaining five pathogens in the slower-than-expected group were all characterized by publication counts in the 1970s and 1980s that outpaced expectations, but subsequently plateaued or decreased. These include pseudorabies (Fig. 2*D*), *P. multocida* (Fig. 3*C*), APP, *Serpulina hyodysenteriae*, and transmissible gastroenteritis virus. All of these pathogens are production diseases whose importance to the industry has declined in recent decades due to better control or even regional eradication. For example, pseudorabies was successfully eradicated from the United States and parts of Europe (17). Regional breakdowns of publication counts reflect the earlier eradication of pseudorabies from the United States relative to Europe (Fig. 3*B*). In addition, changes in management practices in the swine industry beginning in the 1990s led to better control and reductions in the impact of some production diseases. These changes included site segregation, where different stages of production (i.e., farrowing and gestation, growing of weaned pigs, and fattening) occur at different premises, and the transition to all-in/all-out production in which growing and fattening barns/sites are completely emptied of pigs and cleaned before restocking. Due to earlier adoption of these management practices in Northern America, the production impact of diseases such as *P. multocida* may have declined more rapidly in Northern America than in Europe, which is perhaps captured by decreasing research prioritization of this disease in Northern America relative to European publication trends in the past 20 y (Fig. 3*C*).

Role of Intensive Pig Production in Pathogen Prioritization. Throughout this review, it is repeatedly apparent that the industrialization of the pig industry has had profound impacts on pathogen prioritization, which can be observed both in spatial and temporal trends. Intensive swine production has reduced the relative importance of some pathogens while potentially accelerating the importance of others. This general pattern can be observed in the long-term temporal trends as well as through comparing geographic regions with more or less intensive practices (Fig. 4). For example, publications on helminths and protozoa were more common in developing countries, particularly those with a lower percent of the human population living in urban areas, which we use as a proxy for the extent of agricultural intensification (Fig. 4). The reverse is true for bacteria and diseases associated with production, which accounted for a greater proportion of publications in developed countries. Such broad comparisons should not be overinterpreted given that there are many other factors that differ between regions beyond swine production practices, and data on the structure of the swine industry is not available for most countries. However, farm size data are available in Europe and can be used as an indicator of intensive swine production (15). In Eastern Europe, 25–60% of farms contain <10 pigs, whereas ∼90% of farms are >400 head in other parts of Europe (18). It is notable that Eastern Europe is the only European region to include a helminth or protozoal pathogen, *Trichinella*, in its top five, and this may be related to differences in management practices.

There is a general notion that industrialization and globalization of the industry has contributed to the emergence and spread of diseases such as PRRS and PED in the 1990s and 2010s, respectively. However, it is difficult to draw direct linkages from the analysis presented here. Intensification is a gradual process that has occurred over many decades (4), and it would be difficult to disentangle incremental changes in farming practices with other factors at play, including better diagnostics, enhanced surveillance, and growth in research. That being said, there are clear differences in the types of pathogens prioritized between developing and developed countries (Fig. 4). In addition, the implications of large, confined herds and frequent long-distance pig movement for the rapid transmission and spread of pathogens cannot be understated.

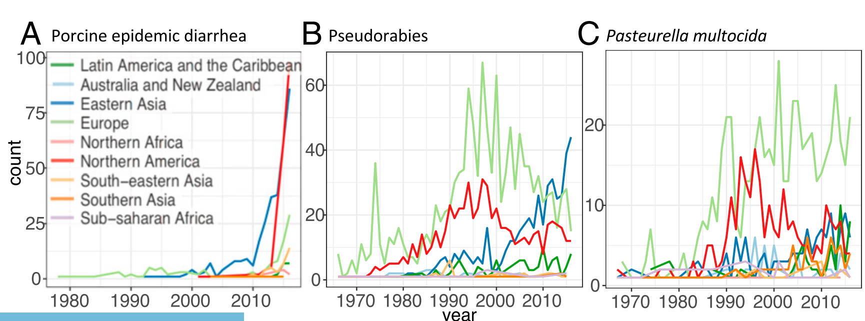

Fig. 3. Publication counts according to geographic region for PED (*A*), pseudorabies (*B*), and *P. multocida* (*C*).

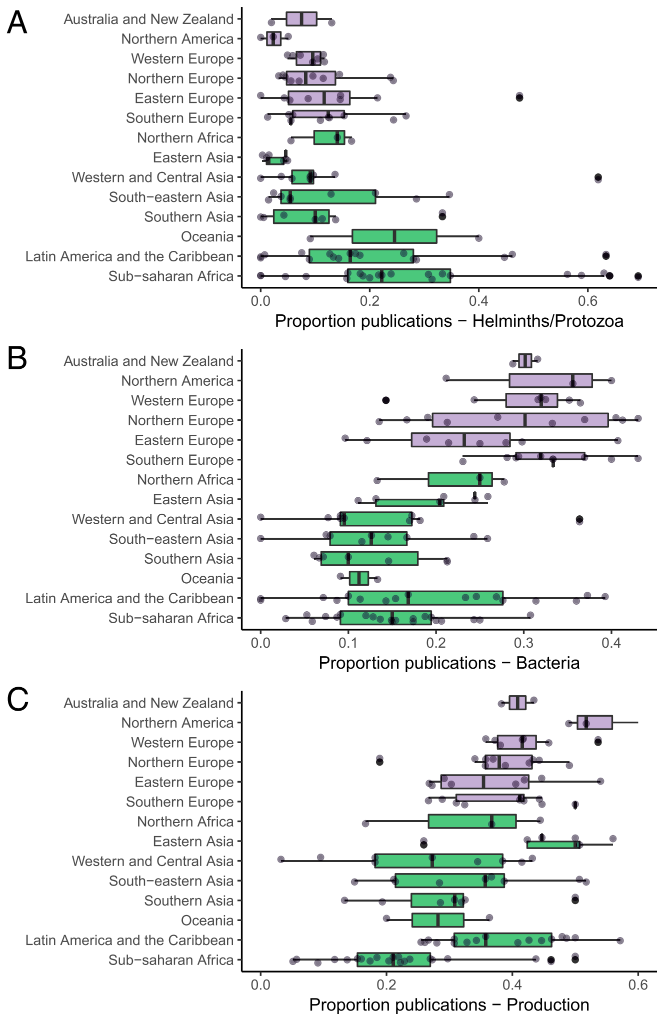

Fig. 4. Proportion of publications in the past 10 y that focused on helminths/protozoa (*A*), bacteria (*B*), and diseases affecting production (*C*). Proportions were calculated for each country and then summarized by region. Colors represent regions with primarily developed (purple) and developing economies (green). Regions are listed in order of the percentage of the human population that is urban, which was used as a proxy for the extent of agricultural industrialization. Proportion of publications by viruses, zoonotic, and reportable pathogens are represented in *SI Appendix*, Fig. S3.

Multinational Collaboration Networks. Fifty countries had at least 30 papers with multinational author lists. Certain regions of the world were underrepresented in the multinational collaboration network, including Western and Central Asia, parts of Latin American and the Caribbean, and much of Africa. For example, there were no countries from Western Africa, and Israel was the sole country represented from Western and Central Asia. Unsurprisingly, the structure of the collaboration network revealed several communities of strongly connected countries that appear to be based on geographic and regional effects (Fig. 5). Each community can be primarily defined as containing members from specific geographic areas: Africa (dark blue), Latin American and the Caribbean (orange), Eastern/Northern Europe (light blue), other European countries (yellow), and Asia/Northern America/Australia (green). Interestingly, the United States and Canada cluster more strongly with Asian countries, such as Japan, China, and South Korea, than with European countries. Mexico, however, is found in a community that includes a number of Spanish speaking countries, such as Spain, Cuba, and Argentina.

To statistically quantify drivers of collaborative linkages, we fit a multivariable exponential random graph model (*ergm*) to the network (19). Our model predicted that authors from two countries were more likely to coauthor papers together if the countries belonged to the same region (coefficient 1.49 ± 0.23 SD), if they shared a common language (0.91 ± 0.21), and if they had a colonial relationship (0.78 ± 0.38, *SI Appendix*). The latter suggests that there is still a strong effect of colonial ties on scientific collaboration networks in agriculture. In addition, we found that countries became more likely to collaborate with increasing annual trade in live pigs (*SI Appendix*, Table S4), and that this metric predicted linkages more strongly than overall trade. This suggests that commercial and supply chain linkages among countries also stimulate scientific collaboration. This effect could also be interpreted in terms of biosecurity, where countries may be more motivated to conduct research on swine pathogens as part of efforts to quantify the risk of disease introduction. New collaborations and data sharing models that are international in scope, span geographical regions, and break historical or language barriers will generate novel linkages and allow the field to take greater advantage of animal health data that is becoming bigger, richer, and more complex (20).

Conclusions. Our review provides a perspective on prioritized swine pathogens over the past 50 y, both regionally and globally. Using publication trends, we document shifting research priorities and place observed trends in the context of regional differences in swine health issues and changing practices in the swine industry. However, an important limitation of this work is that while text-mining algorithms can provide rapid classification and quantification of patterns within large bodies of scientific literature, such methods should not replace researcher scholarship. More detailed scrutiny of publications, such as strain-level information, identification of emerging pathogenic lineages, or categorization by area of research (e.g., epidemiology, control strategies, genetic characterization, diagnostics, vaccine development), will allow for even greater understanding of swine health

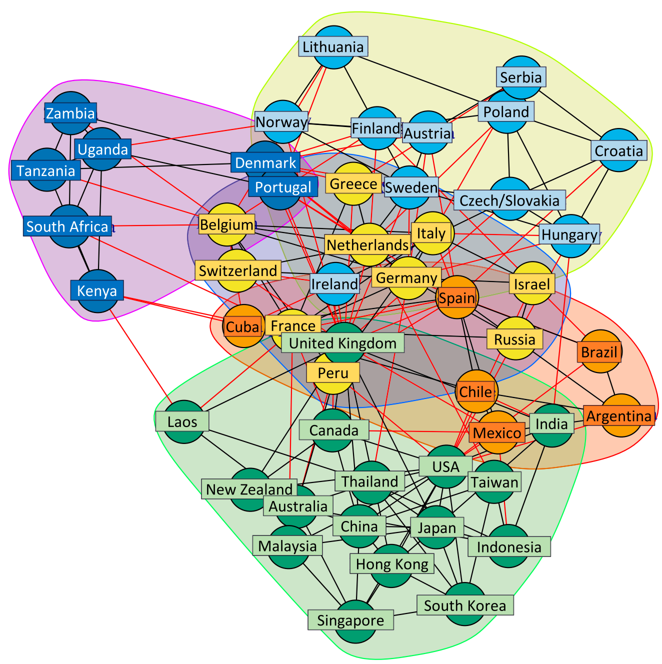

Fig. 5. Multinational collaboration network. Links between countries were weighted according to an index of the frequency with which scientists from those two countries coauthored papers. Clusters represent communities of countries (indicated by color) that tended to coauthor papers with one another more often than with countries outside their cluster.

challenges. For this purpose, the annotated publication database is available at hdl.handle.net/11299/192486.

Temporal trends are sometimes a function of disease emergence, such as for PED, changes in strains and pathogenicity, such as for PRRS, and evolution of effective control measures associated with intensive swine production. Our analysis suggests that more effective control and biosecurity measures associated with intensification have been particularly effective at controlling helminth, protozoal, and some bacterial diseases such as APP. However, current biosecurity methods have in large part been unsuccessful in controlling airborne viruses such as PRRS and influenza, and increases in production scale can be counterproductive in these cases. Since current trends toward intensive production are unlikely to reverse, these production diseases will be an ongoing area of research. In addition, potential zoonoses will continue to be a major focus, with antibiotic resistance in bacterial pathogens growing in importance.

We expect that the results of this scoping review will be useful to veterinarians, epidemiologists, risk analysts, industry organizations, governmental and international animal health agencies, swine production companies, and other groups that require a global outlook to create informed policies, investments, and risk-mitigation strategies in regards to swine health. Given that pathogens are a primary constraint to global swine production and trade, our review is a step in building a more holistic picture of the diverse pathogens cocirculating in swine populations in different regions of the world.

Methods

Literature Search and Database Assembly. We searched the PubMed, Scopus, and Institute for Scientific Information (ISI) databases for each of the top 40 pathogens using the search criteria "(swine OR pig) AND 'pathogen name'". Details of pathogen inclusion criteria are summarized in *SI Appendix*, section 1. PubMed searches were performed in R using the *RISmed* package, which was highly efficient due to the ability to write code to automate and streamline the search. Scopus and ISI searches were performed manually, and publication information and abstracts were downloaded in .bib and .txt files, respectively. To create a data frame with the same structure as the PubMed searches, .bib and .txt files were read into R and the following fields were extracted using the *bibliometrix* package (21): journal; year; title; abstract; author affiliation; and first, second, and last authors. Searches found 47,271, 58,635, and 103,809 documents in PubMed, Scopus, and ISI, respectively, not excluding duplicate documents. A detailed analysis of the comparability of these databases is presented in *SI Appendix*.

This process resulted in 57,471 unique publications. Publications were then assigned to countries by searching for country name variants within the title, abstract, and author affiliation fields. Country name variants included US state names, adjectives representing countries (e.g., British for the United Kingdom), and multiple historic/current variations of country names (e.g., Czech Republic and Czechoslovakia). A full list of the country name variants is included in *SI Appendix*. In this matter, 48,863 publications were able to be assigned to countries. Publications with multiple countries listed within the title and abstract were assigned to all countries. We performed several error checks to estimate error rates associated with various procedures relating to the assembly of the database (*SI Appendix*). All error rates were <3.5%.

Regional and Long-Term Trends. We calculated the annual publication counts by pathogen and by region. Each country was assigned to a region according to the United Nations categories (https://unstats.un.org/home/). Regions with fewer than 100 publications were combined with nearby regions (Polynesia + Micronesia + Melanasia = Oceania; Central Asia + Western Asia = Western and Central Asia). We used generalized linear models (GLMs; Poisson and negative binomial) to evaluate long-term trends in annual paper counts by pathogen, combined with segmented models to identify changepoints in the regression slope (*SI Appendix*).

Multinational Collaboration Networks. We built collaboration networks with countries represented as nodes and links between nodes representing an index of the frequency with which those two countries coauthored papers (Salton index) (22). Countries with <30 multinational papers were not included in the analysis due to small sample size, and we also filtered out links between countries if their Salton index was below the median. To identify clusters of countries that tended to coauthor papers with one another more often than with countries outside their cluster, we applied a weighted community finding algorithm using the Louvain method (23).

We used *ergm*s to investigate the probability of collaborative links in the network as a function of country characteristics and network structure. Here, the outcome was whether an edge occurred between two countries in the network. Potential node-level predictors included region, the country's total swine population (mean live pigs reported annually from 1965 to 2016), land area, gross domestic product (GDP), agricultural GDP contribution (as a percent of total GDP), human population, poverty rate, and whether the county is considered developed or developing by the United Nations. Potential dyad-level predictors included the log annual tons or head of pigs traded between two countries, the log of the overall trade in millions of US dollars between the countries averaged from 1966 to 2016, and whether they shared a common border, official language, nonofficial "common" languages, and colonial relationship. Data sources are detailed in *SI Appendix*, Table S6. Details of model building are included in *SI Appendix*.

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