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Disease ecology in health and medical geography: History, progress, and innovations†

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This paper describes the development of the disease ecology tradition of health and medical geography including some key themes and innovations. It first grounds disease ecology in the history of ecology from the natural sciences and the human ecology traditions within the social sciences. These ecological studies of disease developed in response to limitations in the biomedical approach to studying health and disease that developed after germ theory. While the biomedical approach, which mostly focused on human biology, led to groundbreaking advances in medicine for many decades, it had its limits. Disease ecology applications have modern roots in the decades before and after World War II through colonial and tropical medicine as well as work conducted in an array of other sites, including Nazi Germany, the Soviet Union, and the United States when there were large efforts to create infectious diseases maps and conduct ecological analyses of diseases. Hundreds of disease ecology studies have been implemented on diverse disease systems since World War II. The field progressively broadened in scope, especially during the 1990s and beyond, with several innovations including the application of political ecology approaches to the study of health and disease. Two other recent innovations are summarized through case studies: disease ecology approaches in health intervention research and applications of theory and methods from landscape genetics. The first case study highlights the ecological and geographic heterogeneity associated with the health impacts of drinking-water tubewell interventions in rural Bangladesh. The paper also considers 'landscape genetics' approaches via a case study about influenza that uses modern genetic and spatial tools along with an ecological approach; it describes how the evolution of the virus is related to human-environment-animal interactions. The paper concludes by outlining promising future directions for disease ecology, emphasizing the field's ongoing incorporation of new theories and methods.

Keywords: disease ecology, medical geography, health geography

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Introduction

This paper provides a partial history of the disease ecology tradition of health and medical geography including some of the main themes, debates, and innovations. Our focus here is oriented towards the field in the United States. Although we also consider other sites and traditions, and how scholars based in the United States have interacted with them, inevitably this paper can only offer a partial history. Disease ecology is grounded in the field of health and medical geography, which uses a holistic approach to investigate health and disease. In the United States, the subdiscipline of health and medical

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geography has its modern roots after World War II, when Jacques May became the founding head of the Department of Medical Geography at the American Geographical Society. In those early years, the subdiscipline was almost synonymous with disease ecology. This period of development, however, has historical context in other disciplines and other regions of the world which are important for understanding the development of disease ecology. There have been more recent academic debates about the best path for the subdiscipline of health and medical geography that are also important to understanding the disease ecology tradition of geography. The tradition has seen much progress during the last 75 years and there have been several key innovations, many associated with methodological advances, but also through theoretical development. This paper describes two recent innovations that are offered in two empirical examples. The first is the use of disease ecology theory and methods in health intervention research; an empirical case study of drinking-water tubewell installations in rural Bangladesh is presented. The second theoretical advancement is that of infectious disease ecology approaches in landscape genetics; the empirical example of its application to influenza is presented. These two areas of innovation are just two in the evolving tradition of disease ecology in health and medical geography.

This paper begins with background on ecology from the natural sciences and human ecology from the social sciences, followed by a description of the study of disease before and after germ theory. Next, it provides a partial history of disease mapping as a colonial pursuit by European powers, the Nazis, and the Soviets. The work of Jacques May is highlighted, along with a range of disease ecology studies conducted by other scholars after the field was introduced in the United States. These studies incorporate emerging geographic methods and theoretical approaches, including political ecology. The last sections conclude with case studies on the geography of interventions and the use of landscape genetics approaches.

Ecology, human ecology, and disease ecology

Alexander von Humboldt was an influential contributor to the concepts of ecology in the nineteenth century and is regarded as the founder of biogeography within the field of geography (von Humboldt, 1859). He was a holistic interdisciplinary thinker who considered different components of the natural world as being inter-related. Ernst Haeckel first defined ecology as the study of the relationship of organisms with their environment (Haeckel, 1862). Both Humboldt and Haeckel were contemporaries of Charles Darwin, whose theory of natural selection forms the theoretical foundation for the recent innovation in disease ecology known as landscape genetics, which we discuss later. The term ecology has different meanings in different fields and these meanings have changed over time. The concept of ecology originated in biology and evolved as the field matured, shifting its focus from an emphasis on organisms to an emphasis on relations and functions within systems (Odum, 1969). As the natural sciences developed concepts of ecology, so did the social sciences. The ideas of systems, multiple layers, interactions, and complexity entered sociology as human ecology with roots in the Chicago School of Sociology, which posited that human behaviour is influenced by social structures and not only human biology (Park, 1915; Park & Burgess, 1921; Park *et al.*, 1925; Hawley, 1986). Amos Hawley, who had been trained by one of the founders of the Chicago School, theorized that humans modify their behaviour based on their environment and that they adapt to challenges in their environment when there is disequilibrium. His seminal work on human ecology focused on relationships between individual people and their social groups (Hawley, 1973). As human ecology was practised within the field of sociology, its connection with the natural environment and processes was progressively lost. The focus shifted predominantly to the social environment, although some built environment was occasionally included. Socioeconomic and demographic variables were measured and analysed using new statistical methods that were used to model complex relationships. Socioecological differentiation based on sets of these variables was used to develop theories of socioecological structure. In sociology, political science and other social sciences, including social and urban geography, 'ecology' meant complex, multivariate, quantitative analysis of groups of people and their social, economic, and political conditions. Human-environment interaction included social and political structures with little focus on the natural and built environments. This is not surprising since sociologists, who pioneered this area of study first focused on the urban environment of Chicago. Elsewhere, the concepts of cultural–environmental interactions at different scales of systems were also beginning to be applied to understand infectious diseases in European colonies and later in newly independent tropical countries by Jacques May and others discussed below. In the next section, we discuss the study of disease before and after germ theory leading to the ecological field of medical geography.

Miasma, germ theory, biomedical approach, and medical geography as ecology

Health and medical geography has ancient roots perhaps dating back to Hippocrates (circa 400 B.C.E), who was familiar with the importance of cultural–environmental interactions more than 2000 years ago (Adams, 1886). Place was important to Hippocrates and to the field of medicine until the nineteenth century. Cultural–environmental interactions were regarded as the primary factors influencing disease etiology and health, until germ theory replaced the reigning *miasma* theory (i.e., bad air responsible for disease) in the late nineteenth century, driven by the work of Louis Pasteur, who demonstrated that fermentation is caused by microscopic organisms, and Robert Koch who identified the bacteria responsible for anthrax, cholera, and tuberculosis (Malouin, 1765; Koch, 1881; Pasteur, 1881). The term 'medical geography' was first used by the eighteenth century German physician and infectious disease cartographer, Leonhard Ludwig Finke, who did not understand germ theory and the underlying specific etiology of infectious diseases; his approach had roots in the holistic Hippocratic tradition (Finke, 1792). While there were many medical geography studies being conducted in the pre-germ theory period of the 1850s, the publications of American physician Daniel Drake and German pathologist Conrad Heinrich Fuchs, and others, were increasingly being challenged (Fuchs, 1853; Drake *et al.*, 1854; Barrett, 2000). It had been thought that understanding the geographic patterns of disease might reveal their etiologies, but it was not until germ theory, that major advances in medicine and healthcare could be made.

After German physician August Hirsch developed the 'doctrine of specific etiology', the next decades involved the discovery of bacterium after bacterium (Hirsch, 1883). Many other discoveries followed including sterilization, vaccination, antibiotics, water chlorination, and sewage treatment, all of which dramatically extended people's life expectancies in the developed world. The revolutionary advances that resulted from the doctrine of specific etiology were developed using a biomedical approach which considered mostly human biology and physiology to develop treatments for illness.

However, this approach could not answer all questions because etiology is complex and involves more than just human biological factors. The disease ecology tradition in geography and other ecological traditions in the social sciences developed because while biomedical discoveries led to many life-saving innovations, the model was insufficient to fully understand the complexities of health and disease. Some would say that during this biomedical approach era that followed germ theory, the baby was thrown out with the bath water, and a holistic approach was lost for many decades. With the advent of a disease ecology approach, germs were not considered to be sufficient causes, even for infectious diseases, and attention shifted back to complex ecologies, including environmental contexts and other factors such as human behaviour. As the contradictions between the dominant biomedical approach and the health needs of people increased, the social sciences became increasingly involved. Besides health and medical geography, the decades of the 1960s and 1970s saw the development of the fields of medical anthropology, medical sociology, health economics, and health psychology. The perspective and methods of geography have now formally been applied to the study of health and disease for over 75 years. The modern emergence of interest in health and medical geography is sometimes attributed to the first 'Report of the Commission on Medical Geography (Ecology) of Health and Disease to the International Geographic Union' in 1952 (IGC, 1953). The concept of ecology is central to disease ecology and thus cannot be understood without considering the different theories of ecology in the social sciences and beyond. The following section describes some of the history of early approaches to disease ecology, the genesis of which included disease mapping and the production of disease atlases.

Disease maps and atlases: John Snow, Nazis, Soviets, and colonial medicine

Disease mapping is one component of the history of medical geography as infectious disease maps are the result of ecological thinking and analysis. This section summarizes part of this history starting with John Snow.

Disease maps in the nineteenth century: John Snow

During the nineteenth century there were several scholars who produced disease maps, the most famous of which was John Snow's cholera map around a drinking water source in London in 1854 (Snow, 1855). The clustering of cholera in the vicinity of the Broad Street pump supported Snow's contention that cholera was a water-borne disease; he used this observation to argue that it was a contagious disease, a theory that had not yet been accepted. As the story goes, he had the Broad Street pump handle removed and then cholera declined quickly. Disease mapping has continued and progressed since Snow's time with methodological advancements. While the history of disease mapping is beyond the scope of this paper and is described elsewhere, we offer some examples of disease mapping that were integral to the development of the disease ecology approach (Barrett, 2000; Koch, 2011).

Nazi disease maps and ecology

During World War II, the Nazi regime created maps of many infectious diseases for the large portions of the world that they had designs on conquering. Disease maps were compiled in the '*Seuchen-Atlas*', the Atlas of Epidemic Diseases (Anderson, 1947). The foreword to the Atlas, written by the Surgeon General of the unified armed forces of Nazi Germany, made clear the purpose of the maps. He emphasized that because the soldiers were fighting in many different areas of the world, the illnesses that troops were exposed to were diverse and dangerous, and that it was necessary to understand the distribution of diseases for the war effort. The foreword further stated that the Atlas was intended as a medical resource for military planning, strictly for internal use by military establishments for training of medical students in service of the military, and not for public distribution. The Nazi '*Seuchen-Atlas*' was published from 1942 to 1945 and consisted of 70 black-and-white maps and graphs, and 68 colour maps. It was organized by region including the Near East, Transcaspian Area, Eastern Europe, Baltic Region, Central Europe, Mediterranean Area, and North and West Africa. Examples of maps include: (1) Occurrence of Plague in the Near East, (2) Distribution of Malaria Mosquitoes in the Near and Middle East, (3) Occurrence of Malaria and Distribution of Malaria Mosquitoes in Turkey, (4) Occurrence of Malaria and Distribution of Malaria Mosquitoes in Caucasia, (5) Disease-Carrying Vectors (Other Than Malaria Mosquitoes) in the Near East, (6) Leishmaniasis in the Near East, (7) Leprosy in Iran, (8) Distribution of Rainfall in the Near East, (9) Population Density in the Near and Middle East, (10) Pandemic Spread of Asiatic Cholera, (11) Yellow Fever in Africa, (12) Occurrence of Plague and Distribution of Squirrels West of the Lower Volga, (13) Distribution of Squirrels in Southeast Russia and in the Transcaspian Area, and (14) Tularemia Epidemics in Southeast Russia. The Atlas contents show the result of a huge effort that involved ecological and spatial thinking and supports what we know from history, that one of the goals of the Nazi regime was to conquer vast areas of the world in diverse ecological settings.

Soviet disease maps and landscape epidemiology

After World War II, geographers in the Soviet Union began developing a subfield of medical geography, which culminated in the 'First Soviet Conference in Medical Geography' in November 1962. The conference was attended by 243 delegates from all unions except Latvia, and featured 79 papers (Markovin, 1962; Shkurlatov, 1963; Keller, 1984). Much of the field focused on vector-borne and zoonotic diseases and was aligned with the goals of the Soviet state to expand eastward and extract the Soviet Union's vast resources. The Soviet geographer Eugene Pavlovsky led an effort to explore the vector-borne and zoonotic diseases of the Soviet Union using an approach he termed "landscape epidemiology" (Pavlovsky *et al.*, 1955; Pavlovsky, 1966). Pavlovsky was one of the leading parasitologists of the Soviet Union; he was director of the Zoological Institute of the Academy of Sciences and president of the Geographical and Entomological Societies of the Soviet Union. Because of the importance of the landscape epidemiology approach, he developed the Institute of Medical Geography, which was part of the Soviet Academy of Sciences. Landscape epidemiology had its own unique approach and nomenclature. Pavlovsky introduced the concept of a natural *nidus*, a micro-scale region comprised of a living community within which a disease agent circulates. In this micro-scale region, the habitat conditions maintain the disease system, which includes the agents as well as environmental factors, such as the microecology of soil, vegetation, and animal movement. The Soviet Union was vast and areas such as Siberia were being settled for resource extraction. Hence, understanding what ecosystems could result in human diseases when inhabited was a major goal of this endeavour. It was Pavlovsky's contention that the potential for specific diseases could be identified from the existence of environmental conditions, so that planners could design housing, protective clothing, or work schedules to shield the human population from exposure to infectious diseases. Landscapes and connections with

Russian culture were a central concern for Soviet geographers and landscape epidemiology considered humans and their behaviour to inform planning. By knowing the conditions necessary for specific diseases, Pavlovsky and others in the Soviet Union used landscape to identify disease hazards and therefore develop the basis for landscape modification to prevent disease cycles. While humans were not central to the Soviet disease ecology, humans were part of the ecosystem.

Disease mapping and disease ecology as a colonial endeavour

The political ambitions of countries are often connected to intellectual pursuits as with the Nazis and the Soviets. It is beyond the scope of this paper to provide a detailed historical and theoretical context for such pursuits and how this is intertwined with technocratic endeavours, as others have described, including Deborah Neill's account of the development of tropical medicine within the context of European colonial expansion in Africa (Neill, 2012). However, we should add that other imperial and colonial frames have been an important strand of medical geography. Some of these pursuits led to major discoveries, such as Patrick Manson's contributions in tropical medicine during his work in Asia, that alongside Ronald Ross, was the first to demonstrate that diseases including filariasis and malaria are transmitted by mosquitos (To & Yuen, 2012). In one such example, Kirsch (2023) provides a story of American imperialistic pursuits in the Philippines at the beginning of the twentieth century which involved survey, expedition, spatial data collection, and map making. Tropical medicine has been an important part of United States military pursuits because of the significant morbidity and mortality of its troops due to diarrhoeal diseases, malaria, and many other vector-borne diseases during the wars of the twentieth and twenty-first centuries (Beaumier *et al.*, 2013). Brown and Moon (2004) provide a partial historical context of Jacques May's life which included service in the French army in World War I, as a colonial doctor in Siam and French Indochina, and in the Free French Forces, after the Japanese occupation of Indochina. During World War II, May served as a senior surgeon in the Free French Forces in Singapore, China, Africa, and London, including duties on the immediate staff of General Charles de Gaulle (Fairchild, 1976). He also served as the Chief Surgeon in the Guadeloupe Hospital in the Caribbean, and then emigrated to the United States in 1947 where he helped develop the field of medical geography. This included creating a series of disease maps which have some similar content to the Nazi and Soviet atlases, but on a global scale. While his motivations and the context of his contributions are contested and involved imperial ambitions, he is no doubt an important and prominent figure in the development of medical geography and disease ecology (Brown & Moon, 2004). The following section summarizes some of Jacques May's work as he spearheaded the development of Medical Geography in the United States.

Jacques May

Jacques May initiated the subdiscipline of health and medical geography in the United States with the paper *Medical Geography: Its Methods and Objectives*, developed the first maps of global disease distributions, and wrote an important book titled *The Ecology of Human Disease* (May, 1950, 1954a, 1954b, 1958). This represented the culmination of a long intellectual evolution on May's part. As mentioned above, he began his career as a French colonial physician, spending more than a decade as head of surgery at the major French hospital in Hanoi and as Professor of Tropical Medicine at the Hanoi University Medical School. He started his intellectual journey by questioning why his patients in the tropics experienced disease and responded differently to treatment compared to European settings where he was trained. May's ideas about health and disease progressed towards focusing on his patients' multiple, simultaneous infections and the conditions of their lives. Then, from his own travel and experience in tropical Asia, he came to understand the cultural and environmental conditions that produced and limited his patients' health and disease. May was influenced in his development of disease ecology by the French approach to geography, which emphasized distinctive local-regional expressions of interaction between human and physical environments, expressed as *genres de vie*. He referenced French geographer Maximilien Sorre's concept of 'pathogenic complexes' which posited that physical, biological, and anthropological factors lead to disease (Sorre, 1933, 1947; May, 1950; Barrett, 2000).

Jacques May became the head of the American Geographical Society's Medical Geography Department in 1948. By 1951, he was publishing the first maps of the distribution of diseases, vectors, nutritional deficiencies, and other maps published as inserts in the *Geographical Review*, the journal of the American Geographical Society. His maps included the global distribution of poliomyelitis, dengue, yellow fever, plague, human starvation, rickettsial diseases, Yaws, leishmaniasis, leprosy, malaria vectors, cholera, and many others. They also included descriptions of the ecologies of each of those diseases. For example, in the accompanying narrative on cholera, he described geographic factors such as population density, human mobility, and their heterogeneous spatiotemporal distributions such as 'epidemic' and 'occasional' cholera in different geographic contexts. His version of disease ecology involved multiple dimensions, including human behaviour, natural, and built environment.

In 1960, May left his position at the American Geographical Society and spent the next 15 years working in global public health, mostly focused on combating malnutrition in Africa, Asia, and Latin America. Some might argue that this was part of a neocolonial endeavour, especially since some of the funding for his work came from the United States military. But one could also argue that the military funding was just a means to an end with altruistic intentions and contributions. His disease ecology work continued, including publication of ecological maps and translational research contributions to programs around the world. He worked for the United States Public Health Service, the United States Agency for International Development, the United Nations Development Program, and the World Health Organization. He authored a series of publications on malnutrition, similar to his earlier work on infectious diseases (May & Jarcho, 1961; May, 1963, 1965, 1966, 1967; May & McLellan, 1968, 1972, 1973, 1974). The effort was funded by the Office of Research and Development of the United States Army. He summarized his work in a 1969 publication and stated that his motivation for the work, and for the army funding the work, was that the army predicted a 'world food gap as early as 1955' and that they believed 'that food inadequacies were likely to become a prime cause for unrest and insurgency' (May & Lemons, 1969). His efforts on mapping malnutrition not only included developing inventories for different regions of the world but also identifying holistic strategies for interventions. Similar to his past work, the work was ecological and focused on how food and nutrition programs needed to involve coordinated efforts of health, agriculture, industry, education, and research sectors in combating malnutrition. He died in a car accident along with his wife and co-author, Donna McClellan on 3 July 1975, while conducting work on malnutrition in Tunisia. Jacques May was a disease ecologist to his dying day. One other interesting fact about his life is that he was the father of twin boys born with autism in 1947; he learned that the United States educational system was poorly set up for children with intellectual disabilities and that they were destined for a life in institutions after the age of seven. With his wife at the time, Marie Anne May, he started an innovative, specialized school for children with autism and other intellectual disabilities in Chatham, Massachusetts, which later became the May Institute (May Institute, 2024). His out of the box ecological thinking likely contributed to the development of innovative approaches applied to this important health problem. This legacy continues as the May Institute now operates five special education schools and provides early intervention, home-based, and school consultation services in a dozen states (May Institute, 2024). May led the way for many other disease ecologists' work during the next 75 years, some of which is described in the following section.

Other disease ecologists and parallel development of health services geography

We have described the historical roots of disease ecology and will now offer a few examples of work that followed; the list of contributions is long, and this paper will only scratch the surface. John Hunter, who spent most of his career at Michigan State University, spent decades conducting disease ecology studies on many different infectious diseases and other health outcomes, including river blindness, schistosomiasis, filariases, diarrhoeal diseases, geophagy, influenza, and others (Hunter, 1966, 1973, 1992, 2003; Hughes & Hunter, 1970; Hunter & Young, 1971; Hunter *et al.*, 1982; Hunter & Arbona, 1995). One of Hunter's Master's students, Melinda Meade, who later earned her PhD with Warwick Armstrong at the University of Hawaii, conceptualized a new model of disease ecology known as the "Triangle of Human Ecology". This heuristic model had three vertices—population, habitat (environment), and behaviour—forming a triangle that encompasses the state of human health (Meade, 1977). Population is concerned with humans as biological organisms. The ability of people to respond to insults depends on their genetic susceptibility, nutritional status, immunological status, and physiological status. Habitat is people's environment and includes houses and workplaces, settlement patterns, naturally occurring biotic and physical phenomena, health care services, transportation systems, schools, and governments. Behaviour is the observable part of culture including economic constraints, social norms, mobility, roles, cultural practices, and technological interventions. The Triangle of Human Ecology model differs from sociological models in its separate consideration of behaviour and population. Educational and socioeconomic status are elements of behaviour rather than population. Educational status is behaviour, but the location of a school and its environment are part of people's habitat. In the decades that followed Meade's introduction of the Triangle of Human Ecology model, there have been many scholars who have used this approach. Recent disease ecology studies have been conducted by a new generation of geographers on many different health outcomes and diseases including malaria (Messina *et al.*, 2011; Carrel *et al.*, 2015; Janko *et al.*, 2018a; Janko *et al.*, 2018b), anaemia (Messina *et al.*, 2013), avian influenza (Carrel *et al.*, 2010, 2012; Carrel *et al.*, 2011b), diarrhoeal diseases (Carrel, 2011a; Escamilla *et al.*, 2011, 2013; Winston *et al.*, 2013; Goel *et al.*, 2019, 2020, 2023), and HIV/AIDS (Messina *et al.*, 2010; Carrel *et al.*, 2016). Many of these studies have used modern spatial analytical tools, Bayesian spatial statistics, and genomic methods, but while they might be methodologically more sophisticated than prior eras, they all remain theoretically grounded in disease ecology. Additionally, there are countless other examples not covered here.

While disease ecology studies were flourishing, the 1960s also saw the emergence of locational analysis for health services, starting with studies on regionalization of the Swedish health system by geographers at the University of Lund (Godlund, 1961). At the University of Washington, Richard Morrill, who had completed a postdoc at Lund, became one of the leaders of the 'quantitative revolution' in geography in the United States. He had completed his dissertation on the effects of the transportation system on the use of medical services, and continued with this type of work for decades. He mentored Gerald Pyle and Robert Earickson on their research of health services as part of the Chicago Regional Hospital Studies (Morrill & Earickson, 1968; Pyle, 1971). Gary Shannon and Alan Dever wrote a book called *Health Care Delivery* that first introduced geographers to the subject (Shannon & Dever, 1974). Settlement forms, urban hierarchy, transportation networks, and population mobility had become objects of modeling in urban geography. Pyle conducted a study on heart disease and the spatial dimensions of hospital care in Chicago (Pyle, 1971). He also applied economic geography approaches to the study of the changing processes of diffusion of cholera in nineteenth-century United States, which described how cholera spread was related to changing transportation infrastructure (Pyle, 1969). During this era, advances in spatial analysis were applied to a range of areas, including population movement, settlement hierarchy, and transportation networks. These developments became integral to understanding the ecology of diseases. Other studies included diffusion of influenza, measles, cholera, and hepatitis, as described by Cliff and Haggett (1988) and Thomas (1992). A different aspect of spatial analysis involved the study of the spatial variation of disease occurrence and relationships with environmental and social conditions. These studies have often been classified with disease ecology, but the "ecology" in them was focused more on social factors, and environment was almost an afterthought in many, but not all these studies. The field of medical geography and disease ecology has changed as new theories and approaches have been developed, and the next section describes some of this history.

New areas of inquiry in medical geography and disease ecology

In the early 1990s, there was a theoretical debate within medical geography, with calls to change the name of the field to health geography (Kearns, 1993, 1995; Mayer & Meade, 1994; Mayer, 1996). The debate is described elsewhere, but part of it was about changing the focus of the field away from the dual pursuits of disease ecology and health services, and called for new areas of inquiry that were not historically at the forefront of the field (Brown *et al.*, 2010). New themes included the emergence of 'place' as a framework for understanding health, application of social- and cultural-theoretical positions to health, 'critical' geographies of health, and a focus on well-being and justice (Kearns & Moon, 2002). This suggested 'new' approach to health geography highlighted the concerns underlying the development of social theories. Its proponents mostly employed qualitative methods, in contrast to the predominantly quantitative approaches that had dominated the field of medical geography in previous decades. Critics of these theoretical arguments countered by arguing that the disease ecology framework had always been inclusive of these areas of inquiry; they suggested that those calling for a bifurcation of the field and nomenclature changes were already integral to the field, and that their contributions would broaden and enhance the subdiscipline rather than necessitate a split (Mayer & Meade, 1994; Mayer, 1996).

The issues of social structure and political power had been part of the ecological traditions in the social sciences since before World War II, but few studies in the disease ecology tradition in geography had focused on these issues before the theoretical debate within medical geography in the 1990s. One aspect of the broadening of the disease ecology tradition has been the expansion of studies using a political ecology perspective (Mayer, 1996; King, 2010, 2015; King & Crews, 2013). The development of political ecology is a response to the need to consider the political, social, and economic structures and processes that construct policy and form the context of local and individual exposure to health risks and medical treatment. Political ecology is analogous to political economy but is concerned with more than the consequences of economic production or with power (Brookfield, 2005). Political ecology is explicitly about causal interactions with local ecology. The approach posits that political, economic, and social policies as well as structural institutions and processes are not neutral and are part of the ecology. Political ecology is concerned with understanding how political, economic, and social forces influence choices and actions about the natural environment and resource use. This theoretical framework has been applied to many different health issues, including lead poisoning (Hanchette, 2008), health care delivery (Rosenberg, 1988), and infectious diseases due to refugee crises (Kalipeni & Oppong, 1998). Political ecology is just one example of the broadening applications and theoretical advancements in the disease ecology tradition of geography. Disease ecology will continue to evolve and change with new techniques and theoretical innovations. We offer two such innovations here as case studies in the next two sections, one on the geography of interventions and the other on landscape genetics approaches.

Ecological approaches in intervention research: drinking-water tubewells in Bangladesh

The first theoretical advancement that we discuss is using disease ecology theory and methods in health intervention research. Disease ecology has mostly involved observational studies describing geographic factors related to disease risk. Intervention studies have been limited, although some scholars, including Jacques May with his work on malnutrition, were involved in conducting research and implementing programs based on the research. However, they typically did not formally study the impacts of those interventions and implementation programs. We offer a case study that highlights the value and theoretical contributions of ecological health intervention studies. The intervention is drinking-water tubewell installations in rural Bangladesh for arsenic mitigation. The case study applies spatial Bayesian statistical approaches in conjunction with incorporating intervention theory into disease ecology approaches. The background to this empirical example is that despite widespread availability of improved drinking water sources, diarrhoeal diseases and arsenic poisoning remain major challenges and affect millions of people in rural Bangladesh (Bangladesh Bureau of Statistics and UNICEF Bangladesh, 2019). By the 1990s, compared to traditionally used surface water sources that contributed to high diarrhoeal disease burden, large-scale adoption of shallow tubewells for drinking-water by over ninety-five per cent of rural Bangladeshis had resulted in significant reductions in diarrhoeal disease morbidity and mortality (Caldwell *et al.*, 2003). However, widespread testing a decade later revealed that over a 100 million people may have been exposed to unsafe levels of arsenic due to naturally occurring arsenic in the shallow aquifer tapped by shallow tubewells, prompting a public health emergency (Smith *et al.*, 2000).

Arsenic mitigation efforts in rural Bangladesh have either involved households switching to nearby shallow tubewells determined to be arsenic-safe based on testing results, or to deep tubewells that source drinking-water from deep arsenic-free aquifers (van Geen *et al.*, 2002; Ahmed *et al.*, 2006). During the past two decades, hundreds of thousands of deep tubewells have been installed across rural Bangladesh due to their advantages in providing reliably consistent and arsenic- and microbially-free drinking water at source due to increased depths, as compared to low-arsenic shallow tubewells (Zheng *et al.*, 2005; von Brömssen *et al.*, 2007; Burgess *et al.*, 2010; Ravenscroft *et al.*, 2013; Shamsudduha *et al.*, 2019). However, there are practical concerns regarding accessibility of these sources. Deep tubewells are approximately ten times more expensive to build compared to shallow tubewells (Jakariya *et al.*, 2005), and require many households, which cannot afford these tubewells, to travel farther either to a deep tubewell in another household compound or in public places such as mosques, markets, or schools (van Geen *et al.*, 2016; Goel *et al.*, 2019; Cocciolo *et al.*, 2021). Hence, any protections may be offset during water handling and storage as the people living in households using deep tubewells walk farther on average to their drinking-water source, store water longer, and use microbially unsafe surface water sources more frequently for other non-consumption tasks (Goel *et al.*, 2019, 2020). As a result, using deep tubewells may instead be associated with higher microbial contamination at point-of-use (Goel *et al.*, 2023) and may instead increase the risk of diarrhoeal diseases among populations in rural Bangladesh (Lokuge *et al.*, 2004).

Intervention studies evaluating health risks of deep tubewell use in Bangladesh have reported contrasting results. Deep tubewell use, compared to shallow tubewell use, was found to be associated with significantly reduced diarrhoeal disease incidence in Matlab, Bangladesh, an area highly affected by groundwater arsenic contamination (Escamilla *et al.*, 2011; Wu *et al.*, 2011; Winston *et al.*, 2013). However, in another highly arsenic-affected part of Bangladesh in Barisal District, switching to a tubewell greater than 300 meters deep was associated with increased mortality, suggestively due to increased microbial contamination and diarrhoeal diseases (Buchmann *et al.*, 2023). Although intervention studies evaluating health effects of deep tubewells are limited, these contrasting results require further attention to examine why deep tubewell interventions have different impacts across the two study settings. This example suggests that such interventions are influenced by their geographic context. Understanding how interventions are affected by their context—defined as potential social, economic, environmental, or even political characteristics that may affect intervention development and implementation—is crucial in determining how they work, why they fail, and whether they can be adapted from one context to another (Craig *et al.*, 2018).

Population health intervention research (PHIR) is a research framework that 'aims to capture the value and differential impacts of interventions, the process by which they create change, and the contexts within which they work best (Hawe & Potvin, 2009). Unlike traditional monitoring and evaluation approaches to population health interventions, the PHIR framework goes beyond focusing on only the 'pattern' of whether an intervention had an impact or not. Instead, the research framework emphasizes quantifying the heterogeneity in the impact of a population health intervention, uncovering the mechanisms that drive the effect of the intervention, and quantifying the conditions under which the positive effects of a population health intervention are maximized (Potvin, 2016). Health and medical geographers are well situated to use geographic methods in conjunction with the PHIR framework and help uncover the ‘process’, and not just the ‘pattern’ that drives the efficacy of population health interventions (Harrington *et al*., 2016).

Our case study research was conducted in rural Matlab, Bangladesh from March 2018 to October 2019. We conducted community-based diarrhoeal disease surveillance of all households with children under five years old that used either a shallow or deep tubewell for drinking-water. In total, community health workers made over 100 000 visits, covering 22 750 households across 142 villages, collecting information about household drinking-water source, under-five diarrhoeal disease incidence and tubewell location and ownership. By combining these data with comprehensive demographic, geospatial, and socioeconomic data as part of the large scale long-running Matlab Health and Demographic Surveillance System (Alam *et al*., 2017), we were able to both account for important confounders and examine the effect of deep tubewell interventions across a large population to uncover effects that may otherwise not be possible to detect. We examined the geographic ‘context’—referred to as the relevant population, environmental, and behavioural characteristics that may influence the effectiveness of deep tubewell use on diarrhoeal disease incidence.

Controlling for important confounding factors, we found that under-five children in households that used a deep tubewell for drinking-water had 17 per cent lower diarrhoeal disease risk (95 per cent CI: 29 per cent to 4 per cent) compared to children in households that use shallow tubewells for drinking-water (Goel *et al*., unpublished data). Deep tubewells were most protective in households that procure drinking-water outside their compound, in households located in flood-prone areas, and the protection was highest during the dry season. While such analysis highlights important contextual or place-based effects associated with heterogeneity in intervention effectiveness, it is often not possible to measure all relevant observable features of the context related to an intervention. It is well-established among geographers, including health and medical geographers, that relationships between predictors and outcomes often exhibit spatial non-stationarity and are not constant across space (Brunsdon *et al*., 1996; Fotheringham *et al*., 2003). In this case study, we combined methodological developments in multilevel modeling that measure contextual intervention effects and local regression models that incorporate spatially-varying coefficients to examine whether the effectiveness of deep tubewell interventions against diarrhoeal diseases differed across space and what underlying contextual processes might be driving those differences (Janko *et al*., 2019). We built a model evaluating deep tubewell intervention effectiveness against diarrhoeal diseases to account for unmeasured contextual effects and spatial heterogeneity by using Integrated Nested Laplace Approximation (INLA) and stochastic partial differential equations (SPDE) (Rue *et al*., 2009; Lindgren *et al*., 2011). Specifically, in addition to adjusting for confounders and household compound level random effects, we included both a spatially varying intercept, and spatially varying slopes for the effect of deep tubewell use on diarrhoeal diseases. The spatially varying intercept term borrows information from neighbouring georeferenced household compound locations and highlights any residual unmeasured contextual effects that may be spatially structured. By adding a spatially varying slope term for the effect of deep tubewell use, we could map the spatial distribution of the odds of diarrhoeal diseases associated with deep tubewell use as compared to shallow tubewell use across Matlab.

We found that there is spatial heterogeneity in deep tubewell effectiveness across Matlab, with some areas also exhibiting increased odds of diarrhoeal disease associated with deep tubewell use compared to shallow tubewell use (Figure 1A). While the spatial patterns of diarrhoeal disease odds are important by themselves and highlight important areas where interventions do not have intended benefits, they also help generate additional hypotheses about potential underlying or contextual effects and processes that may be driving the observed patterns. By observing the spatial distribution of diarrhoeal disease odds and mapping the distribution of households using deep tubewells (Figure 1B), we hypothesize that diarrhoeal disease incidence may also be linked to the density of deep tubewell use, i.e. the proportion of neighbouring households that use deep tubewells at a given location. While we do not statistically examine these effects, it is possible that in addition to the effect of individual use of deep tubewells on diarrhoeal disease incidence, there may be additional 'neighbourhood' effects. For example, if a large proportion of neighbouring households use deep tubewells, there may be added protection against diarrhoeal disease incidence due to availability of more microbially safe water at source, and better access due to potentially denser deep tubewell networks.

A spatial disease ecology approach helps us understand the spatially heterogenous effect of deep tubewells on diarrhoeal disease incidence because of spatially heterogenous ecological factors. The ecological approach to intervention research that is presented brings a PHIR framework and advanced spatial statistical analysis to the field of disease ecology. The approach applies a geographic lens to PHIR research by focusing on the complex ecology that results in heterogeneous spatial ecological effect of interventions. The spatial data and modern spatial methods available now are something that Jacques May, and his contemporaries did not have available to translate their disease ecology studies to public health practice. While we argue that there is a paucity of research in the geography of health interventions, there have been several geographers who have applied these concepts to nutrition, HIV/AIDS, dengue, malaria, chronic

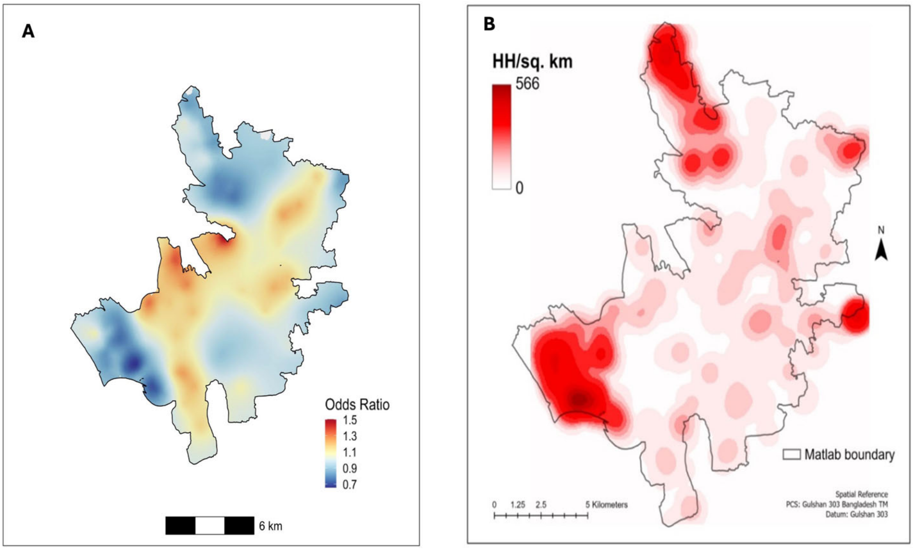

Figure 1. *A) Map displaying the odds ratio of deep tubewell use on under-five diarrhoeal disease incidence compared to shallow tubewell use. B) Map displaying the number of households using deep tubewells per square km in Matlab.*

disease, and others as described in Harrington *et al.* (2016). However, there is a great need to expand the contributions of health and medical geography towards translating our observational research into public health practice. We have much to offer as a discipline and subdiscipline to research on interventions with our spatial ecological theory and methods. The next section offers another example of an innovation in disease ecology through landscape genetics.

Landscape genetics of influenza case study

The second case study is on the landscape genetics of influenza. We first describe the landscape genetics approach, followed by a summary of prior work on avian influenza in Vietnam (Carrel *et al.*, 2010, 2012; Carrel *et al.*, 2011b), and a case study of swine influenza in the United States. Most infectious disease ecology studies have primarily focused on disease incidence or prevalence. Landscape genetics studies focus on spatial distributions of genetics of pathogens, and ecological drivers of the genetic variation and evolution of pathogens. Humans exist in a state of dynamic equilibrium with their environments, and in order to understand disease, we need to understand both people and places (Hunter, 1974). However, this focus on people and places overlooks pathogens, which are the root cause of infectious diseases. Pathogens are evolving and changing, just as people and places are, due to human-environment interactions. As pathogens experience selective pressure and differentially adapt in different ecosystems, we need to consider the pathogen as a function of people living in places within ecosystems (Carrel & Emch, 2013). The theory and methods to integrate a pathogen component into disease ecology is relatively new. It is only during the past two decades that genetic methods such as calculating genetic relatedness as divergence from an ancestor, or identifying mutations such as drug-resistant genes, became widely available to apply to this area. Phylogeographic analysis incorporates both phylogenetic and geographic approaches together whereas landscape genetics incorporates genetic, spatial, and ecological approaches together.

Darwin described how different landscapes in the Galapagos Islands were associated with different finch beak shapes and sizes (Darwin, 1859). Geographers have applied these concepts in biogeography, such as in Waldo Tobler's research on the morphology of plants as a function of distance in New Zealand (Tobler *et al.*, 1970). Landscape genetics is a subfield of landscape ecology that combines that field with population genetics. Landscape ecology is focused on understanding how patterns in the landscape influence processes of organisms in that landscape (Turner, 1989). Examples of patterns include the arrangement of different types of land cover or fragmentation of landscapes. Using landscape genetics to consider the evolution of human pathogens in a landscape is a recent extension of the approach beyond plants and animals. Integrating disease ecology theory on population and environment interactions with population genetics data and methods from landscape ecology allows us to answer questions that were not possible before (Carrel & Emch, 2013). For instance, we can start to understand how and why pathogens spread and evolve across landscapes, what places are conducive to pathogens evolving quickly, and what interventions might slow or prevent disease emergence. These concepts have been applied in studies of the landscape genetics of influenza.

Carrel *et al.* (2010, 2011b, 2012) applied a landscape genetics approach to the study of avian influenza. Highly pathogenic H5N1 avian influenza has persisted in poultry and human populations in Asia since 2003. It has since spread to wild and domestic bird populations in the United States, and as of 2024, has been detected in cattle as well as cattle farm workers who handled infected livestock. Building on research that explored the types of populations and environments that were conducive to incidence, a landscape genetic analysis in Vietnam revealed that in areas with aquaculture, with high human population densities, and low socioeconomic status, H5N1 avian influenza viruses had the highest rates of evolution (Carrel *et al.*, 2012). The combination of susceptible hosts, places where there is high interaction between hosts, and socioeconomic status all drive genetic variation. High rates of evolution results in a greater number of opportunities for the virus to mutate making more efficient human-human transmission more likely.

For swine influenza, the ecological drivers of the genetic variation of the virus are different than for avian influenza, although the ecosystems of avian, swine, and human influenzas intersect and there is gene flow between the systems. While avian influenza in Vietnam is associated with bird distributions and socioeconomic status of the human populations, swine influenza is more related to agricultural networks and gene flow between different levels of the ecosystem including farm, farm systems, landscape, and regional level factors. Pigs are a crucial part of influenza A (IAV) virus disease ecology. Pigs, with both avian-like and human-like receptors, act as 'mixing vessels' for reassortant viruses (i.e., those that have undergone genetic reassortment) (Ma *et al.*, 2008) and can contribute to genetic segments of pandemic IAVs. In particular, the 2009 H1N1 pandemic in humans, also referred to as the 'Swine flu' pandemic was caused by the A(H1N1)pdm09 strain which spilled over from pigs to humans, and had segments of human, avian, swine influenza lineages (Smith *et al.*, 2009). Over the past decade, the A(H1N1)pdm09 virus has diversified within swine populations globally, leading to numerous novel reassortants through diversification of the IAV genetic pool and further fueling concerns of novel pandemic IAV viruses spilling over into humans (Ducatez *et al.*, 2011; Nelson *et al.*, 2012, 2015).

This concern of dynamic and rapid potential for IAV genetic evolution and reassortment in pigs is further fueled by the unique ecology of domestic swine production systems in countries such as the United States and China. In the United States, which is the second largest pork producer in the world after China, and accounts for approximately 11 per cent of worldwide swine production, swine are produced in multisite coordinated production systems that maximize desired animal traits and weight gain (Kaplan *et al.*, 2015). These systems have largely phased out farrow-to-finish operations that performed all growth-phases of swine production and instead consist of multiple farms operating in tandem, with each farm responsible for one stage of the production process or life cycle of pigs. A unique aspect of these systems is that they are closed, meaning there are no introductions of animals from outside the system. Each farm or site within the system has a specific purpose, such as raising replacement female pigs, or breeding and raising piglets for meat production, or gestating and farrowing sows to raising to the point of weaning replacement breeding stock. This unique multisite system creates interconnected swine transportation networks between farms, particularly those within the same swine production system. As a result, these highly connected small number of swine intensive farms that account for pig movements within may be at higher risks of both receiving and spreading infections (Valdes-Donoso *et al.*, 2017; Moon *et al.*, 2019). Additionally, long-distance swine transportation networks associated with large-scale commercial swine production may facilitate the rapid spread of diseases across geographic boundaries (Walia *et al.*, 2019; Hatuwal *et al.*, 2024). Understanding the patterns of IAV evolution related to swine movements and the ecology of swine production systems is crucial as such interconnectedness exposes commercial swine farms to IAV infections from multiple sources which can facilitate emergence of novel swine IAV reassortants (Gonzalez-Reiche *et al*., 2017; Makau *et al*., 2021)

As part of an ongoing study, we obtained 940 geocoded IAV genomic sequences from archived diagnostic samples from ten different states between 2007 and 2021 from the Disease Bioportal hosted at the Center for Animal Disease Modeling and Surveillance (CADMS) (Perez *et al*., 2011). Most of these sequences were collected in the Midwest, particularly in Illinois and Iowa, across five major swine systems (Figure 2). Based on the location of the sequences, these multisite coordinated production systems exhibited different spatial arrangements. Systems such as A and D were relatively geographically clustered, while some systems such as B and E exhibited wide geographical spread across multiple states. Notably, while these systems are closed and distinct, some sites within different systems have geographical overlap, as observed among the closely located sites in systems C and E in Iowa (IA).

Additionally, we observed the circulation of multiple clades (natural genetic groups) of IAV across the systems during the study period (Table 1). The most dominant clades were gamma, which was derived from the classical swine influenza lineage, and delta1, which was derived from the seasonal human influenza lineage. Other clades have also been detected. Notably, while some clades have continually been detected across the past 15 years, others have either not been detected or emerged later. For example, gamma, delta1, and delta2 were continually detected across the 15-year period, while beta has not been detected since 2015. Similarly, the alpha clade, which was detected in 2009–10, was again detected in 2016 and onwards. The npdm clade, that emerged

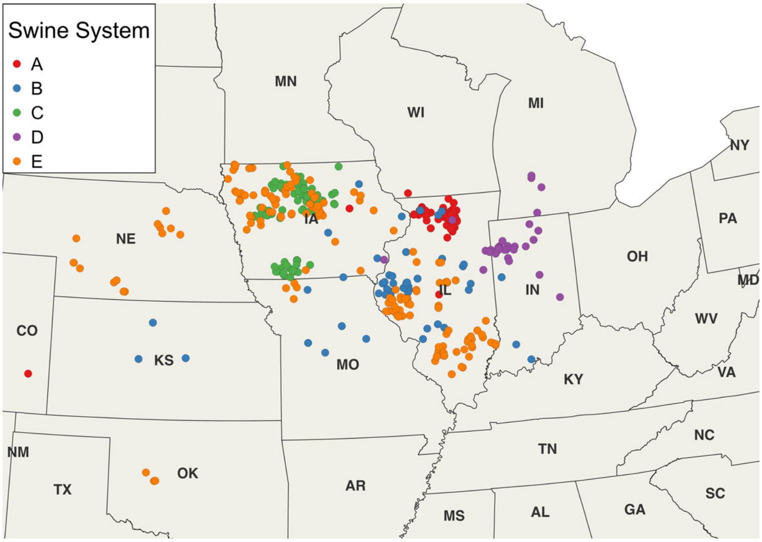

Figure 2. *Map displaying the distribution of swine influenza A (sIAV) viral sequences by swine production systems. Systems have been labelled from A to E to preserve anonymity.*
Source: Data were obtained from the Disease Bioportal hosted at the Center for Animal Disease Modeling and Surveillance (CADMS).

Table 1. **Frequency distribution of IAV clades from 2007 to 2021.**

Clade	General Description	Frequency %
gamma	Classical swine flu lineage. Result of a triple reassortment event between H3N2, H1N2 and H1N1 viruses.	336 (36%)
delta1	Seasonal human flu lineage. Emerged from human IAV introduction into swine in early 2000. Contains both H1N1 and H1N2 swine influenza viruses.	265 (28%)
delta2	Seasonal human flu lineage. Contains H1 and N1 genes, highly divergent from delta1.	131 (14%)
npdm	2009 swine flu pandemic clade. Transmitted from swine to human and back to swine.	96 (10%)
alpha	Classical lineage. Related to the 1918 human influenza pandemic that circulated from 1930s to current.	63 (7%)
beta	Classical lineage. Developed due to reassortment events between classical H1N1 isolates and H3N2 viruses in pigs.	49 (5%)

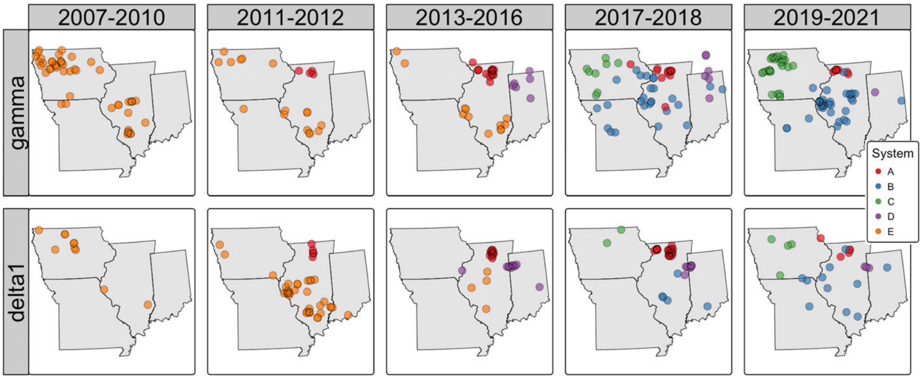

Figure 3. *Spatiotemporal distribution of gamma and delta1 clades across the US Midwest from 2007 to 2021 stratified by dominant swine production systems.*

as a result of the 2009 Swine Influenza pandemic, has been detected in the domestic swine populations since its introduction.

Given the differences in geographic arrangements of sites within different swine production systems and the circulation of multiple different IAV clades across time, we conducted an exploratory analysis to examine the spatiotemporal distribution of IAV clades across swine production systems from 2007 to 2021. We compared the spatiotemporal distribution of the 2 dominant clades, gamma and delta1, that accounted for 65 per cent of the total samples in our dataset. For both clades, we observed strong clustering of clades by system (Figure 3). During 2007–10, gamma was only observed in system E across both Illinois and Iowa, potentially reflecting the role of pig flows in transmission within systems, even across longer distances. In 2011–12, gamma was also observed in sites within system A in northern Illinois, followed by more detection in system A and D sites. By 2019–21, the gamma clade was detected across other systems as well. In the case of delta1, we observed similar patterns of spread within systems, but detection was more spatially clustered, potentially suggesting that proximity to sites may also have played a role, in addition to swine movement networks.

To further examine whether swine systems or geographic distances play a role in IAV gene flow, we calculated pairwise genetic distances (p-distance) for all IAV H3 subtypes based on the genetic sequences. H3 is a type of protein (known as hemagglutinin or HA) that is responsible for binding the virus to the infected cell. Hence, any genetic changes in the protein can either decrease or increase the ability of the virus to efficiently bind and infect. The genetic distance is a measure of genetic similarity or differences between two samples and can help provide an indication of how genetically different specific influenza strains may be from each other. The p-distance is one measure of genetic distance, which determines the proportion of nucleotide sites at which the two sequences are different. By comparing genetic distances with geographic distances between sequences, we can identify how space may either promote or prevent gene flow and determine the underlying processes that drive or hamper gene flow. In this case study, we compared correlations between pairwise genetic distances and geographic distances for sequences that were within the same swine production systems, and for sequences that were in different swine production systems (Figure 4). We observed that there is no detectable correlation between genetic distance and geographic distance among sequences within the same system, potentially suggesting that despite large distances between some sites within the same swine production systems, the constant movement of pigs and IAV viruses limits genetic variation. However, we noticed a more classic ‘isolation by distance pattern’ where genetic distance increases with geographic distance while comparing pairwise sequences across different systems. This means that H3 hemagglutinin genes in sites that are in proximity but in different systems are more genetically similar as opposed to sites further away. Hence, these results suggest that despite being presumed closed systems, there may be viral transmission across systems through sites in proximity. While we are not able to measure the potential pathways directly, this finding suggests that differences in biosecurity measures and movement of swine workers within sites across different systems may play a role in transmission.

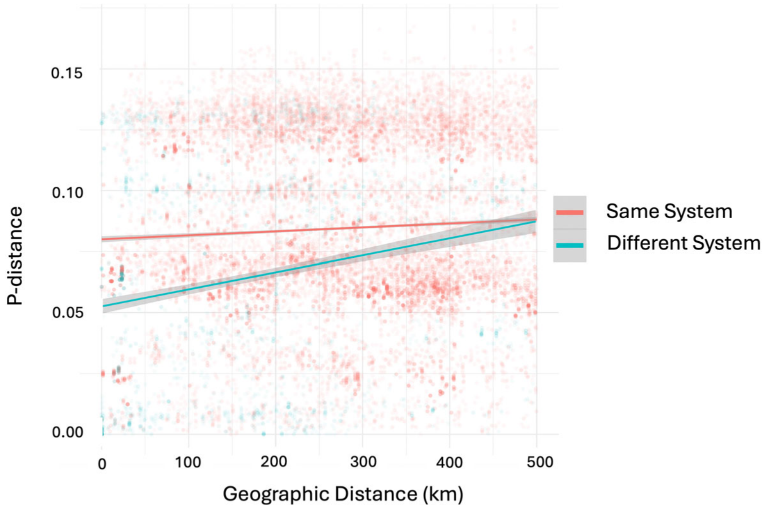

Figure 4. *Correlation of pairwise genetic distances (p-distance) and geographic distances between H3 sequences within the same swine production systems and different systems.*

This second empirical example of landscape genetics on pathogens utilizes modern genetic and spatial tools along with an ecological approach to understand the ecological drivers of the evolution of the influenza virus. The largest pandemic in the twentieth century was the 1918 influenza pandemic which infected an estimated third of the global population and killed an estimated 50 million people (Johnson & Mueller, 2002). While the largest pandemic of the twenty-first century so far has been the Covid-19 coronavirus pandemic, many infectious disease specialists including the authors of this paper believe the most likely next pandemic will be caused by an influenza virus once again. Understanding the drivers of the evolution of influenza pathogens requires an ecological approach and this knowledge can help prevent or help limit its spread.

Conclusions

The disease ecology tradition of health and medical geography has ancient roots and has evolved with many influences from both the social and natural sciences. The development of the field has involved multiple layers of context, including the integration of various technologies of different eras, with the backdrop of different state goals around the world in different historical periods, some quite nefarious. During the past 75 years, the field has grown to be more inclusive of different perspectives and approaches, and there have been many innovations, including applications that move beyond observational studies focused on health interventions, and the application of spatial and ecological landscape genetics approaches in infectious disease studies. There have been many other innovations that draw from several interdisciplinary theoretical and methodological approaches, and there have been hundreds of disease ecology studies conducted. Some explicitly ascribe to this branding, and some do not, but all are influenced by the theoretical history of disease ecology, even if the authors of such studies are sometimes unaware of these roots.

There are many promising areas of disease ecology that can be developed further to answer the most important research questions of our time. There are usually political and economic factors that comprise the underlying structural determinants of health and disease. Geographers have the methodological skills to advance the political ecology approach through our spatial and integrative lens that holistically involves humans and environments. Environmental justice studies that use an ecological approach is one such promising area since unequal distributions of environmental burdens are by their very nature, spatial and ecological problems. As described in the first case study, most disease ecology studies in geography have been cross-sectional observational studies describing disease risk. Moving beyond observations of risk towards studies that determine the impact and effectiveness of interventions is a ripe area of research. Additionally, more focus on longitudinal studies can overcome many of the limitations of cross-sectional studies and can help elucidate causal relationships. While some work that uses aggregate health outcome data is relevant, some questions can only be answered using individual health outcome data that integrate geographic context into models so that underlying mechanisms of the disease ecology of individual health can be ascertained. Many of the infectious diseases that disease ecologists study, such as malaria, cholera, dengue fever, Zika virus, and chikungunya are climate sensitive. Incorporating climate variables and climate change into disease ecology studies for these diseases and other health outcomes is an obvious extension to this field and must be interdisciplinary and should involve collaborations with climate scientists. The disease ecology tradition of health and medical geography will also continue to evolve via new methods. Artificial intelligence approaches such as machine learning and deep learning will be incorporated into the field in many ways, for both explanatory and predictive purposes. For example, machine learning models can integrate and process big data from various novel data streams such as cell phone data to study human mobility or use model-based geostatistical approaches to create spatial risk surfaces, all of which can be included in disease ecology models. There are many other new geographic methods that can be employed in disease ecology studies, including those that have not yet been developed.

The field of disease ecology in health and medical geography will continue to progress and incorporate new geographic methods and approaches. One of the early practitioners of disease ecology in the United States, John Hunter, saw it as an integrative perspective that required all the questions and methodologies of geography's various traditions. In 1974, he wrote a paper setting forth the essential challenge of medical geography (Hunter, 1974). The challenge to geographers was that they contribute to health studies using diverse approaches and methods from the breadth of the field and all its subdisciplines. We believe this challenge is being met and the health and medical geography tradition of disease ecology will continue to progress and thrive into the future.

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