GeoHealth

RESEARCH ARTICLE
10.1029/2024GH001296

Special Collection:
Climate change and infectious diseases

Key Points:

- We investigated the role of wild bird migration in the inter-continental spread of avian influenza on a global scale
- We analyzed the global poultry trade data to highlight how human economic activities intersect with disease dynamics
- Our findings indicate that both the poultry sector and wild bird migrations significantly contribute to avian influenza transmission

Supporting Information:

Supporting Information may be found in the online version of this article.

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Citation:
Jindal, M., Stone, H., Lim, S., & MacIntyre, C. R. (2025). A geospatial perspective toward the role of wild bird migrations and global poultry trade in the spread of highly pathogenic avian influenza H5N1. *GeoHealth*, *9*, e2024GH001296. https://doi.org/10.1029/2024GH001296

Received 3 DEC 2024
Accepted 30 JAN 2025

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A Geospatial Perspective Toward the Role of Wild Bird Migrations and Global Poultry Trade in the Spread of Highly Pathogenic Avian Influenza H5N1

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Abstract This study presents the interplay between wild bird migrations and global poultry trade in the unprecedented spread of highly pathogenic avian influenza, particularly the H5N1 clade 2.3.4.4b strain, across the world and diverse ecosystems from 2020 to 2023. We theorized the role of migratory birds in spreading pathogens as various wild bird species traverse major flyways between the northern and southern hemispheres. Simultaneously, we analyzed the global poultry trade data to assess its role in H5N1's anthropogenic spread, highlighting how human economic activities intersect with natural avian behaviors in disease dynamics. Lastly, we conducted spatial hotspot analysis to identify areas of significant clustering of H5N1 outbreak points over different bird families from 2003 to 2023. This approach provides a strong framework for identifying specific regions at higher risk for H5N1 outbreaks and upon which to further evaluate these patterns with targeted intervention studies and research into what is driving these patterns. Our findings indicate that both the poultry sector and wild bird migrations significantly contribute to global H5N1 transmission, which helps better understanding of H5N1 transmission mechanisms when combined with ecological, epidemiological, and socio-economic perspectives. The results are intended to inform policy-making and strategic planning in wildlife conservation and the poultry trade to improve public health and animal welfare globally.

Plain Language Summary The unprecedented scale and simultaneous infection of avian influenza across multiple species raise concerns about the potential threats to human health, especially in the upcoming years, if not months. The looming increase in bird migrations to the south adds a layer of complexity and urgency to the situation. As we navigate this evolving landscape, it becomes imperative to closely monitor and comprehend the altered dynamics of the virus to implement effective strategies for mitigating the risks associated with human infections. In this study, we tracked the movement of some wild birds according to their seasonal migration along with the incidence of avian influenza. While the spread patterns revealed that the avian influenza had started in Asian countries, it is not clear how it spread from Asia to Europe because, with the birds we analyzed, it was unable to find a flyway from Asia to Europe. However, every spread after the first incidence of avian influenza in Europe can be correlated with the seasonal migration of birds from one country to the other. Europe to Greenland to North America to South America can be established with different wild birds along with the spread from Europe to Africa.

1. Introduction

The avian influenza virus (AIV) has undergone significant evolutionary advancements over the decades, exhibiting cycles of outbreaks and dormancy. There have been repeated outbreaks of avian influenza H5N1 since 1997 in different parts of the world affecting poultry, wild birds, mammals, and humans. In poultry, highly pathogenic influenza A virus subtype H5N1 infections lead to severe clinical symptoms such as respiratory distress, reduced egg production, and high mortality rates, often resulting in economic losses due to mass culling (Kanaujia et al., 2022). Among wild birds, the virus causes neurological symptoms, lethargy, and death, impacting migratory populations and ecological systems (Scarpa et al., 2023). Mammalian infections, including in species such as seals, minks, and domestic cats, have been associated with respiratory illness and fatalities, often raising concerns about cross-species transmission (Leguia et al., 2023). In humans, H5N1 infection is rare but can cause severe respiratory illness, with a mortality rate of approximately 60% in confirmed cases since it emerged in 1997, underscoring its significant public health risk (WHO, 2007).

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Historically, AIV has been a persistent zoonotic threat, with its initial significant outbreak attributed to the highly pathogenic avian influenza (HPAI) H5N1 strain in 1997 in Hong Kong. This event marked a pivotal shift in understanding the virus' potential for cross-species transmission, as it led to 18 human infections with a mortality rate of 33% (Claas et al., 1998). Subsequent outbreaks in 2003–2004 affected poultry and wild birds across Southeast Asia, eventually spreading to Europe and Africa following mass die-offs of migratory birds at Qinghai Lake, China (Blagodatski et al., 2021; Chen et al., 2005).

The 20th century witnessed three significant pandemics—Spanish flu (1918, H1N1), Asian flu (1957, H2N2), and Hong Kong flu (1968, H3N2)—underscoring AIV's potential for reassortment and rapid global dissemination. AIV's resurgence in 2014–2015 highlighted its capacity for extensive intercontinental spread, predominantly via migratory birds and international poultry trade (Seeger et al., 2021). Between 2016 and 2017, H5 strains reappeared in Asia and Europe, affecting both wild birds and poultry populations, with ongoing outbreaks continuing into the 2020s. The virus's ability to adapt to wild birds and mammals has significantly complicated containment efforts, as environmental shedding, migratory bird pathways, and seasonal reintroductions continue to drive transmission dynamics (Kanaujia et al., 2022; Scarpa et al., 2023).

Migratory birds, especially waterfowl, are central to AIV's global spread, serving as reservoirs and vectors for the virus. These birds traverse continents during seasonal migrations, creating opportunities for interspecies transmission at stopover sites and in overlapping habitats with domestic poultry. The fecal-oral route is a key transmission mechanism, facilitated by the persistence of AIV in water bodies under favorable conditions (Olsen et al., 2006). The virus' genetic diversity is amplified through interactions among migratory and resident birds, enabling the emergence of novel strains with heightened virulence or transmissibility (Scarpa et al., 2023).

Recent outbreaks from 2020 to 2023 highlight the growing complexity of AIV transmission. HPAI H5N1, initially detected in wild birds in Europe, spread rapidly across Africa, Asia, and the Americas. The unprecedented geographic range of the virus, including its emergence in South American marine mammals such as sea lions, and penguins, underscores the role of migratory birds in facilitating long-distance dissemination (Leguia et al., 2023). Phylogenetic analyses suggest that migratory flyways act as both sources and sinks for AIV, enabling intercontinental movement and environmental transmission (Zhang et al., 2023). However, questions remain regarding the precise pathways and mechanisms involved, particularly in the context of mammalian infections and potential spillover events.

Given these challenges, our research investigates the role of migratory birds in the spread of AIV. The study aims to elucidate the spatial and temporal patterns of virus transmission, focusing on migratory flyways, interspecies interactions, and environmental shedding. To achieve this, geospatial techniques and machine learning models are employed to analyze the outbreak data, migration patterns, and ecological factors influencing virus spread. By understanding these dynamics, the study seeks to inform surveillance strategies and control measures to mitigate the global impact of avian influenza.

2. Who Is Responsible for the Spread of AIV?

The debate over the role of migratory birds in the dissemination of AIV has evolved significantly over time. Early investigations into AIV spread primarily identified poultry trade as the dominant factor. Until the early 2000s, wild bird infections were sporadic and largely attributed to virus circulation within domestic bird populations (Gauthier-Clerc et al., 2007). Reports suggested that migratory birds were victims rather than vectors of AIV, and their involvement in transmission remained contested.

2005: *Turning Point at Qinghai Lake*: In 2005, the understanding of AIV transmission dynamics began to shift dramatically. A mass die-off of wild birds at Qinghai Lake, China, marked a pivotal moment in the study of migratory birds' role in spreading the virus (Chen et al., 2005). The outbreak, which coincided with the migration timelines of Bar-headed Geese and other waterfowl, resulted in the westward spread of H5N1 to regions such as Russia, Turkey, and Croatia. Genetic tracing linked outbreaks in at least 61 countries to the virus that emerged at Qinghai, indicating a connection between migratory pathways and virus dissemination (AO/OIE/WHO, 2011).

However, questions persisted. The discovery of artificially reared Bar-headed Geese at Qinghai Lake raised doubts about whether the virus spread was primarily driven by wild bird migrations or infected farmed birds. Additionally, the virus' failure to significantly impact key wintering countries such as India, Pakistan, Australia, and New Zealand introduced uncertainty about the role of wild birds as vectors (Canavan, 2019). An alternative theory emerged, suggesting that while the geographic spread aligned with bird migration routes, regional amplification might be attributed to infected poultry movements (Peiris et al., 2007).

2006–2010: *Global Expansion and New Hypotheses*: By 2006, the virus had reached Europe, with the number of affected countries growing from 16 to 55 within a year, including nine reporting human fatalities (Canavan, 2019). The spread of H5N1 across continents spurred investigations into the interplay between migratory birds and human-assisted poultry movements. While some studies correlated the geographic expansion with migratory flyways, others highlighted the role of stopover sites where virus transmission could be amplified by diverse host interactions. This dual pathway theory of migratory bird movements and regional poultry trade became central to understanding AIV dissemination (Peiris et al., 2007).

Post-2010: *Renewed Attention on Wild Birds*: After 2010, evidence increasingly pointed to wild birds as significant contributors to AIV spread. The unprecedented global transmission of H5N1 from 2020 onwards further highlighted their role. After 2020, reports of HPAI outbreaks in mammals, including Spanish minks, otters in England, and sea lions in Peru, underscored the environmental persistence of the virus and its transmission across diverse hosts (Nishiura et al., 2023). Whilst waterfowl have typically been the vectors of long-distance transmission of AIV, H5N1 2.3.4.4.b has infected over 130 new species of non-waterfowl birds. For the first time, simultaneous outbreaks in wild birds, poultry, and mammals across multiple continents were documented, reinforcing the hypothesis that migratory birds play a critical role in intercontinental virus dissemination.

Despite advancements, critical gaps remain in understanding the precise mechanisms by which AIV is spread across long distances. Key questions include:

- How do specific migratory flyways facilitate virus transmission across continents?
- What role do stopover sites and host diversity play in strain evolution and amplification?
- To what extent do environmental factors (e.g., frozen fecal matter, water salinity, and temperature) influence virus survival and persistence?

Our study aims to address these deficiencies by focusing on the spatiotemporal dynamics of AIV spread through migratory flyways. By leveraging geospatial techniques and analyzing migratory bird patterns in relation to outbreak data, we seek to clarify the interplay between bird migration, poultry trade, and environmental shedding. This research will provide insights into the long-distance transmission mechanisms of AIV and inform strategies for surveillance and containment.

3. Methodology

This study embarked on a comprehensive examination of disease outbreak patterns with a specific focus on data post-2005. The methodology employed high-resolution outbreak data, trade route reconstruction, and migratory bird analysis with advanced spatial and statistical techniques to address the research objectives.

3.1. Data Set

The data set of our study was sourced from the World Animal Health Information System (WAHIS), a platform maintained by the World Organisation for Animal Health (OIE). WAHIS serves as a repository for globally reported cases of animal diseases, with updates provided daily by member countries. The availability of data extends back to 2005, offering a rich longitudinal data set for analysis. For our study, we concentrated on a specific period from January 2020 to September 2023. Our analytical focus was narrowed to instances of the H5N1 genotype and cases of H5 (N untyped), thereby ensuring a targeted examination of data relevant to our research objectives. This refined approach allowed for a comprehensive analysis of trends and patterns associated with these specific avian influenza genotypes within the selected timeframe.

To complement our analysis of avian influenza patterns, we also reconstructed poultry trade routes based on documentation provided by the International Poultry Council (IPC). The IPC represents the global poultry meat industry and serves as its authoritative voice, compiling and distributing vital information regarding poultry trade dynamics. This reconstruction of trade pathways allowed us to investigate potential correlations between international poultry trade activities and the geographical spread of avian influenza cases, enriching our understanding of how trade practices may influence disease dissemination across borders.

3.2. Data Visualization and Analysis

This study examines the migratory patterns of several wild bird species which have been newly infected by H5N1 clade 2.3.4.4b, including the Bar-tailed Godwit, Black-tailed Godwit, Great Sand Plover, Pacific Golden Plover, Eastern Curlew, Red Knot, Common Crane, Northern Fulmar, Great Pelican, Peregrin Falcon, White Stork and the traditional vectors of AIV, waterfowl. These birds engage in intercontinental migrations, predominantly in two seasons: breeding and wintering.

During the breeding season, which spans from late February to almost late July, these avian species inhabit the northern hemisphere. The breeding grounds are diverse and include Arctic regions of Eurasia, Alaska, Iceland, northern Russia, Siberia, Canada, Greenland, Norway, the Netherlands, and more. As the northern regions experience colder temperatures in the winter months, the birds initiate their migratory journey, traveling along eight major flyways to reach warmer wintering grounds in the southern hemisphere. The wintering grounds encompass West Europe, Africa, Australia, New Zealand, Southeast Asia, Hawaii, the Middle East, and other regions. This migration serves as a vital adaptation to the changing seasons, allowing these wild birds to optimize their chances of survival and reproduction.

In addition, the poultry trade data and H5N1 incidence rates are integrated to assess their collective impact on the spread of AIV. By examining the interplay between wild bird migrations, global poultry trade practices, and the incidence of H5N1, we endeavor to elucidate the multifaceted dynamics of AIV's intercontinental transmission and identify significant factors that have influenced its global dispersion.

A bar graph spanning from 2005 to 2023 was created to visualize the frequency of the avian influenza cases over the study period, identifying trends, cyclicality, and significant changes in outbreak patterns. Stacked bar charts were generated to depict the annual distribution of outbreaks across continents, facilitating a comparative analysis of geographical variations in outbreak occurrences. These visualization techniques aid in understanding how the burden of avian influenza is distributed globally and identify the continents that may require targeted surveillance and control measures.

The use of distinct visualization styles for bird migration and poultry trade routes serves to highlight the unique nature of these two transmission mechanisms. A global approach was necessary to represent the migratory flyways of wild birds, which span multiple continents and often connect regions separated by vast distances. In contrast, poultry trade is regionally focused, with distinct trade hubs and corridors unique to Asia, Europe, and Africa. Each region was mapped separately to provide a clearer understanding of the trade dynamics within these geographical contexts. By isolating these regions, we could better analyze the role of poultry trade in AIV dissemination and distinguish it from the global patterns associated with bird migration. This approach ensures that the maps are not overcrowded, allowing for a more precise interpretation of trade-related virus transmission dynamics.

To investigate the differential impact of AIV across domestic and wild species, we aggregated the outbreak data into two broad categories: domestic poultry and a combined group of wild birds plus mammals. This approach compares the effect of AIV on these distinct populations. To visually represent the proportion of outbreaks affecting each group annually, we utilized stacked bar charts. This method allowed us to depict the relative share of domestic versus wild species impacted by AIV over time.

Outbreak data was sorted to identify countries with the highest number of reported cases. Countries were ranked based on the cumulative number of outbreaks. By examining the countries most affected by avian influenza, we were able to pinpoint hotspots of disease activity and potentially underlying factors contributing to these patterns.

Finally, we conducted spatial hotspot analysis to identify areas of significant clustering of HPAI H5N1 outbreak points over different bird families from 2003 to 2023. We applied Getis-Ord Gi*, a measure for finding spatial clusters in epidemiological data. The Gi* statistic is defined by Equation 1:

$$G_i^* = \frac{\sum_{j=1}^{n} w_{ij}x_j - X\sum_{j=1}^{n} w_{ij}}{S\sqrt{\frac{n\sum_{j=1}^{n} w_{ij}^2 - \left(\sum_{j=1}^{n} w_{ij}\right)^2}{n-1}}} \tag{1}$$

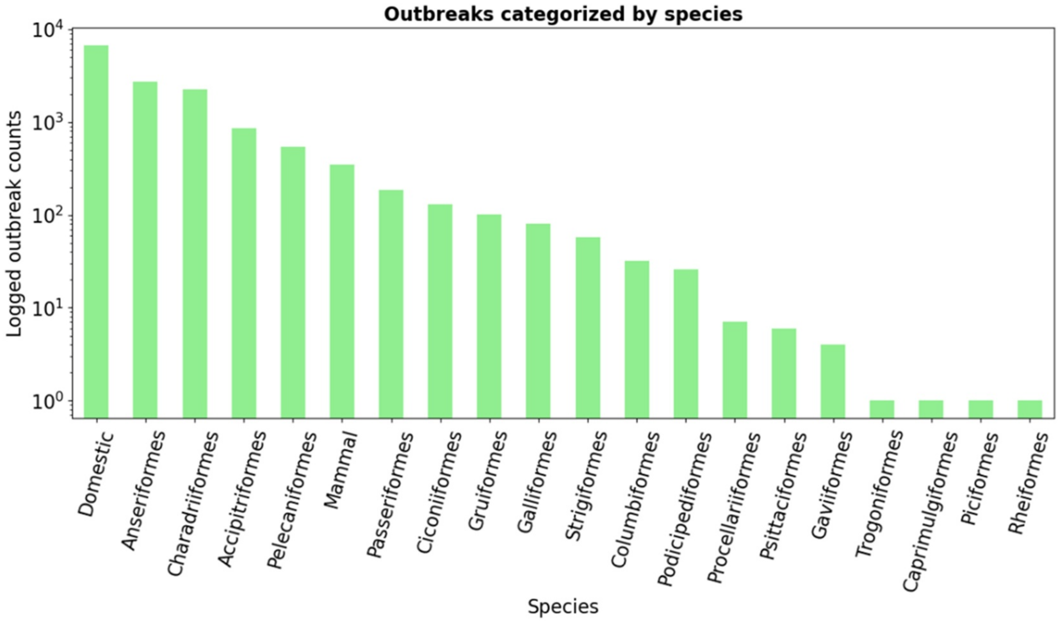

Figure 1. Frequency of outbreaks in the affected species.

where x_j represents the attribute value (in this case, the residuals from a linear regression model), w_{ij} is the spatial weight between locations i and j (in this case, the inverse distance between the two locations), $\overline{X}$ is the mean of the attribute values, and S is the standard deviation of the attribute values. The obtained Gi* statistic detects hotspots (areas having more than expected values) and coldspots (areas having less than the expected values) at various confidence levels. This method has been demonstrated in the past with epidemiological data to study disease patterns and analyze the impact of environmental and ecological factors on disease mapping (Getis & Ord, 1992; Ord & Getis, 1995).

Different environmental variables—air temperature, precipitation, soil moisture, specific humidity, surface pressure, wind speed, global temperature anomaly, vegetation index, and bird abundance—were used in a generalized regression model to determine their influence on H5N1 incidence. After model evaluation, only three variables—soil moisture, wind speed, and bird abundance—were found to be statistically significant in predicting the disease coldspots and hotspots. To ensure the residuals of the model followed a normal distribution, we applied a logarithmic transformation to the dependent variable, which adjusted the distribution and allowed us to achieve a more normal spread of the residuals, as confirmed by the histogram (Refer to Text S2 in Supporting Information S1).

4. Results

4.1. Wild Bird Migration Routes, Poultry Trade and H5N1 Incidence

To understand the global shift of avian influenza from Asia to Europe, The Americas, and Africa, we examined wild bird migration patterns. It aims to elucidate the role of migration in the disease's intercontinental transmission. Initially, species such as waterfowl (e.g., Anseriformes, including ducks, geese, and swans) and Charadriiformes (such as waders, gulls, and auks) were considered primary vectors. However, data from WHO, upon categorization by bird families (Figure 1), revealed that Pelecaniformes (e.g., cormorants and pelicans) and Accipitriformes (notably the Eurasian buzzard, peregrine falcon, hawks, and vultures), also play significant roles in AIV spread. This highlights an expanding host range, indicating the need for broader surveillance across avian taxa.

Figure 1 illustrates the frequency of AIV outbreaks across species groups, with logged outbreak counts demonstrating the dominance of domestic poultry as the most affected group, followed by Anseriformes and Charadriiformes. This trend highlights shared water sources acting as hotspots for fecal-oral transmission.

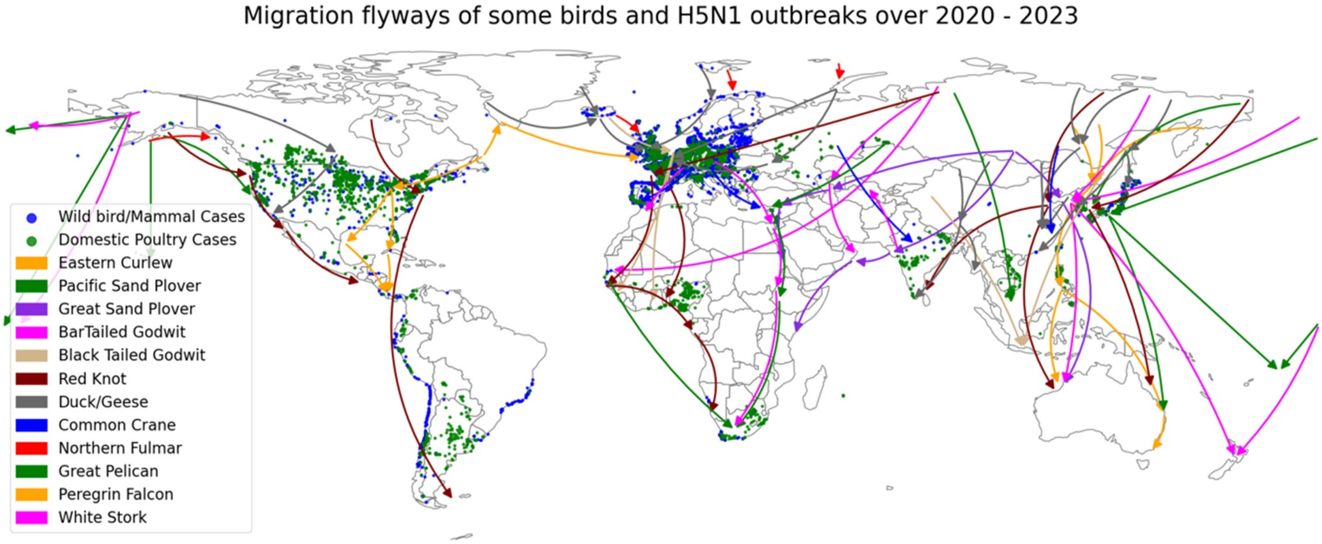

Figure 2. Wild bird migration patterns and the H5N1 outbreaks.

Mammalian hosts, although ranked lower, reflect concerning spillover events, raising questions about interspecies dynamics.

Tracking migration patterns using spatial mapping (Figure 2) reveals the interconnected pathways of wild birds and their overlap with AIV outbreak hotspots. The map uses distinct hues to represent different bird species and their flight path, providing a visual representation of their contribution to AIV dissemination. Blue markers denote outbreaks in wild birds or mammals, while light green markers indicate cases in domestic poultry. The spread of H5N1, as depicted in Figure 2, demonstrates a closely interconnected pattern. Transmission originates in Europe and extends to Greenland. From Greenland, it subsequently progresses to North America and South America. At the same time, a parallel dissemination pathway is observed, extending from Europe to South Africa.

The spatial clustering of outbreak points aligns with the stopover and breeding grounds of migratory birds. This is particularly evident in regions such as northern Europe and Russia, which serve as breeding sites for species like ducks, geese, and cranes. North Africa and the Middle East also show significant clustering, as they are critical wintering and stopover zones. These regions coincide with both wild bird outbreaks and poultry farm infections. Similarly, East Asia, including China, Japan, and Korea, exhibits a dense network of domestic poultry outbreaks and wild bird cases. This pattern suggests a complex interaction between wild bird migration and poultry farming in these areas.

Building on the analysis that highlighted the impact of AIV across a wider range of species than previously recognized, as depicted in Figure 1 and illustrated in Figure 2, this study shifts its focus toward a comprehensive examination of the migration patterns and disease spread among wild bird populations. The objective is to gain a deeper understanding of the role that various avian species play in facilitating the intercontinental and ecological propagation of AIV.

The Common Crane, typically breeding in Russian and European regions, migrates southward to northern Africa, central India, and east China for wintering. In November 2021, some of these cranes were found deceased in France, and from December 2021 to January 2022, instances of Common Cranes exhibiting neurological symptoms, leading to death, were reported in Israel. This suggests that the cranes might have been infected in Europe before commencing their migratory journey, with symptoms intensifying en route, potentially spreading the disease to Israel and other stopover sites.

The Northern Fulmar, a resident of the North Atlantic and Arctic, feeds mainly on fish and marine life. In June 2022, deceased individuals were discovered across Sweden, Denmark, the UK, and the Faroe Islands, indicating a significant, widespread impact in its habitat. This trend was mirrored in the case of the long-eared owl, a non-migratory species affected in Europe in early 2022 and later detected in North America by year's end, suggesting transmission through other species. These incidents underscore the complexity of disease spread among avian

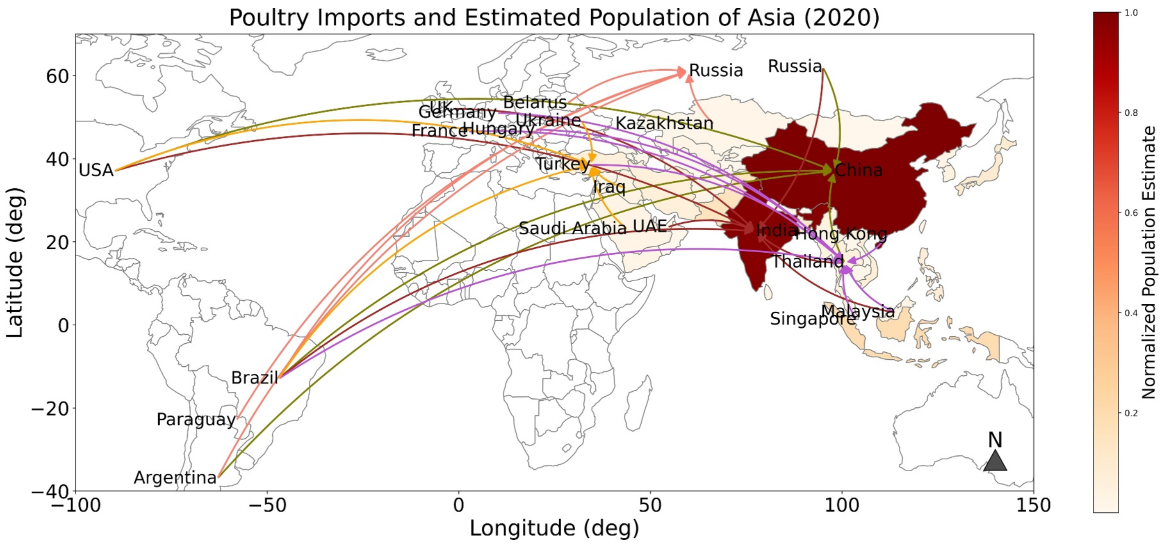

Figure 3. Poultry trade in Asia.

populations, extending beyond migratory behaviors to impact a broad range of species across extensive geographical areas.

The sequence of events concerning pelican species infections and fatalities closely aligns with their migratory patterns and seasonal movements across various regions. The initial outbreak among the Great White Pelicans in early 2021 across Senegal and South Africa, followed by occurrences in Russia during their northward breeding migration, illustrates a concerning trend. This pattern persisted with their southward migration, evidenced by deaths in Israel. Similar incidents among Dalmatian Pelicans in Greece and Romania during March 2022. Subsequent deaths were recorded in Peruvian Pelicans in late 2022 and by early 2023 Brown Pelicans were affected along the coasts of Panama, Costa Rica, and Honduras. This highlights a widespread and complex challenge, underscoring the need for comprehensive avian health monitoring and research to understand and mitigate these occurrences.

The Peregrine Falcon, a long-distance migratory bird traveling from Europe to Greenland and North America, saw numerous sickness and mortality reports in Europe in early 2022. By May 2022, a case was confirmed in the US, with additional incidents noted in Japan toward the end of 2022 and the start of 2023. Despite the bulk of reports emerging from Europe, this does not imply that the US was unaffected, highlighting the global impact on this species. Similarly, the White Stork, migrating between Europe and Africa, exhibited a parallel trend of health issues, with European cases reported early in 2022 and an incident in South Africa by February, indicating a widespread concern across their migratory pathways.

Following the analysis of avian species' roles in spreading AIV, we now examine the impact of the global poultry trade. By analyzing graphical data, this aims to highlight how poultry trade contributes to AIV's spread, integrating the roles of natural vectors and human activities in the virus' transmission. The Figures 3–5 use different colors to represent the volume of poultry imports for each country, as indicated by the gradient on the legend. Darker shades, such as deep red, signify higher import volumes, with countries like China being major importers. Lighter shades, transitioning to pale orange, indicate lower import volumes. This color-coding helps visually differentiate the import levels across countries. Additionally, a distinct single color is used for all import routes leading into a specific country. For example, all import routes into China are represented using olive.

Figure 3 indicates the dense poultry trade in India and China from various places including islandic countries. Originally, the large-scale outbreaks of H5N1 started with poultry in Asia, mainly India and China from 2020 onwards, escalating to widespread European cases by late 2020. As noted many bird species migrate northward for their breeding season and stay there during the months usually spanning from February to September and again migrate back southward for their wintering season. Migratory patterns of ducks, geese, and waterfowl from South Asia to Europe, particularly for breeding seasons, are identified as initial vectors for AIV spread into

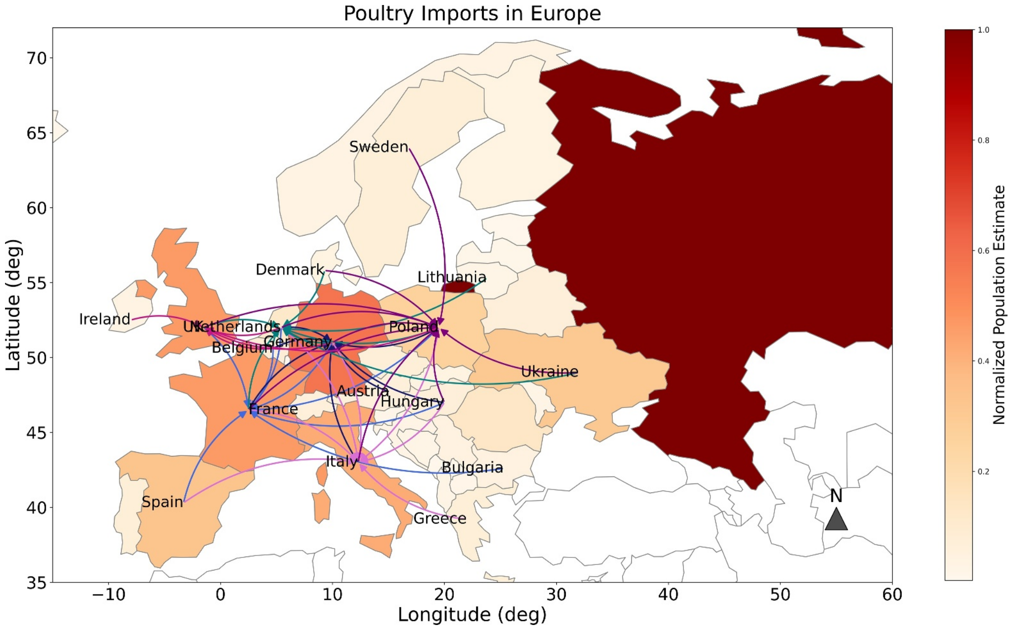

Figure 4. Poultry trade in Europe.

Europe. Subsequent intra-European dissemination is attributed to poultry trade, significantly impacting Africa and North America (Figure 4). Initial AIV reports in Africa, particularly from poultry in Nigeria (late 2020), underscore the role of European poultry trade in spreading AIV (Figure 5), with wild bird cases (cormorants, geese, etc) emerging from mid-2021 onwards. In early 2021, Senegal reported instances of the Great White Pelican exhibiting signs of illness, a development that corresponds with their established migratory routes from Europe to Africa, as depicted by the green arrows in Figure 2.

The introduction of AIV into North America has been largely linked to the natural migratory patterns of wild birds from Europe through Greenland. Initial detections of affected Anseriformes to Accipitriformes were on Canada's

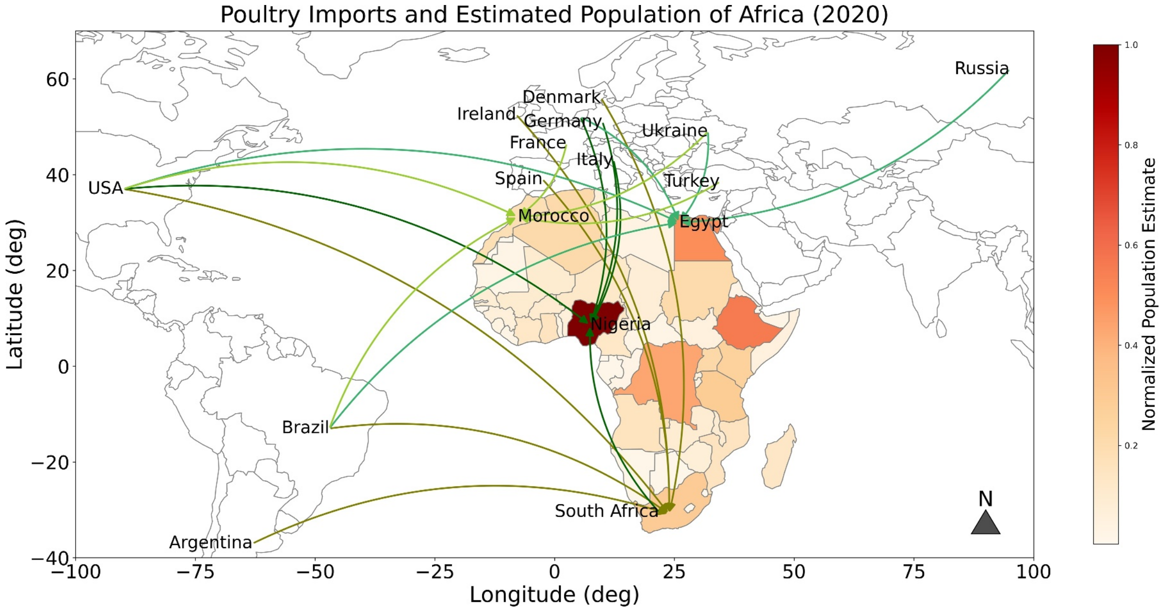

Figure 5. Poultry trade in Africa.

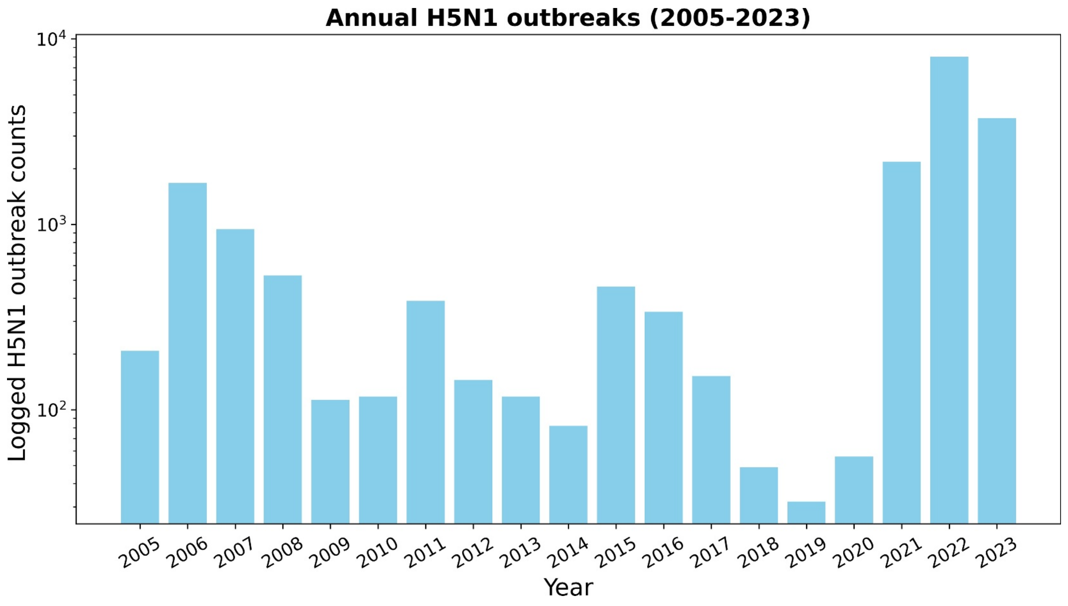

Figure 6. Annual incidence of H5N1 outbreaks from 2005 to 2023.

eastern coast between late 2021 and early 2022 and quickly expanded across the continent. The virus spread from the eastern to the western parts of Canada and the US toward the north by mid-2022. The direction of the spread is indicative of the fact that it was due to birds because wild birds usually travel and reside in the north during this time for their breeding period. By October 2022, initial AIV detections in Colombia involved Anseriformes, with falcons and pelicans in Mexico, Chile, and Peru, coinciding with their southward migratory routes as depicted in Figure 2. Early February saw the virus impacting South American mammals, notably with sea lion fatalities along Chile's coast. Subsequently, domestic avian cases emerged in Argentina, Bolivia, and Uruguay. By May 2023, Charadriiformes cases were recorded along Brazil's coast, illustrating the comprehensive spread of AIV across avian and mammalian species in South America.

These developments illustrate the effect of complex transmission dynamics encompassing both natural avian migration and human-influenced trade activities on the spread of avian influenza.

4.2. Frequency of H5N1 Avian Influenza Outbreaks

In our preliminary analysis of disease patterns spanning the 20th century, we examined outbreaks occurring since 2005. Upon closer inspection of Figure 6, a distinct pattern emerged, revealing peaks in outbreak occurrences every 5 years. This temporal frequency was evident in the notable outbreak years of 2006, 2011, 2015, and 2021, suggesting a cyclicality in the reemergence of the disease.

4.3. Continent Share of Frequency of H5N1 Outbreaks and Cases

Our analysis indicates a persistent increase in H5N1 outbreaks from the initiation of the ongoing outbreak in late 2020, with a noticeable increase from 2021 into 2022. Figure 7 indicates substantial regional differences in outbreak occurrences. Europe and Asia exhibit ongoing and consistent outbreaks across the entire timeframe, highlighting these continents as primary regions of concern. The lower frequency of reported cases in Africa could be misleading, potentially reflecting underreporting or insufficient testing rather than a true decline in outbreak frequency. The right-hand scales of both the annual and monthly graphs display the counts of species found dead (shown in red) and those culled (shown in blue) as containment efforts. The peak of culling (Figure 8) actions coincides with the highest number of reported outbreaks in 2022, indicating an intense response to control the spread of the virus. Many poultry farms in the US culled millions of poultry animals in early 2022 to contain the outbreaks of AIV. However, the persistence of the outbreaks suggests that these measures may not have been fully effective. Additionally, outbreak reports from South America over time, hint at the spread of the virus across

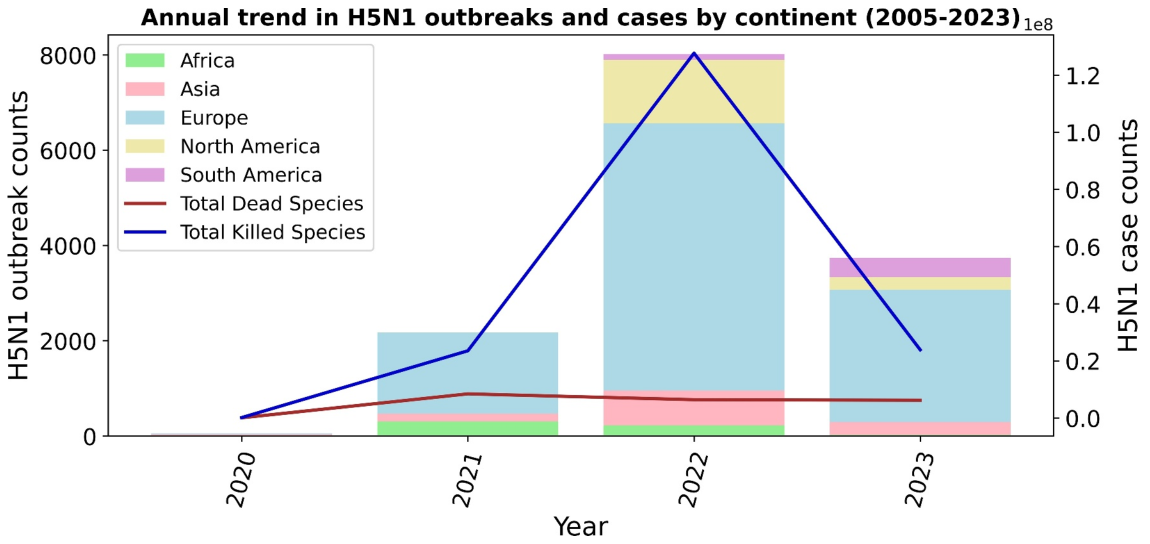

Figure 7. Annual frequency of H5N1 outbreaks and cases from 2020 to 2023 stacked by country.

continents from 2020 to 2023. This warrants further investigation into migratory patterns and trade routes that may influence the spread of the H5N1 virus.

4.4. Species Share of Frequency of H5N1 Outbreaks and Cases

Figure 9 reveals significant insights into the disparate impact of AIV across different species, illustrating the profound effects on domesticated and wild species populations. The domestic birds comprise over half of the outbreaks reported. The graph underscores that the crisis is not confined to domesticated birds alone; a significant fraction of the cases involves wildlife. This portion includes a wide spectrum of wild birds and mammals, highlighting AIV's reach beyond farm settings and into natural ecosystems. Such findings are critical as they hint at the complex dynamics of AIV transmission, which involves both managed and natural habitats.

While the graph depicts fewer cases in wild species, it is essential to consider the potential for underreporting in these populations. The surveillance of wildlife diseases is challenging, and the actual number of wild species affected could be higher. The incidence of AIV in wildlife also raises concerns about the natural reservoirs of the

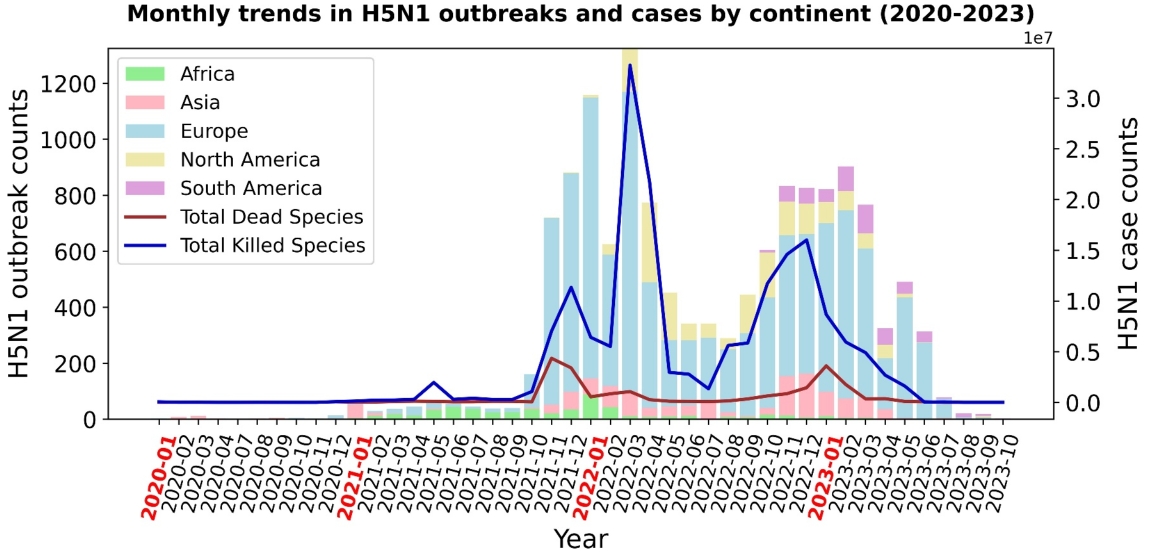

Figure 8. Monthly frequency of H5N1 outbreaks and cases from 2020 to 2023 stacked by country.

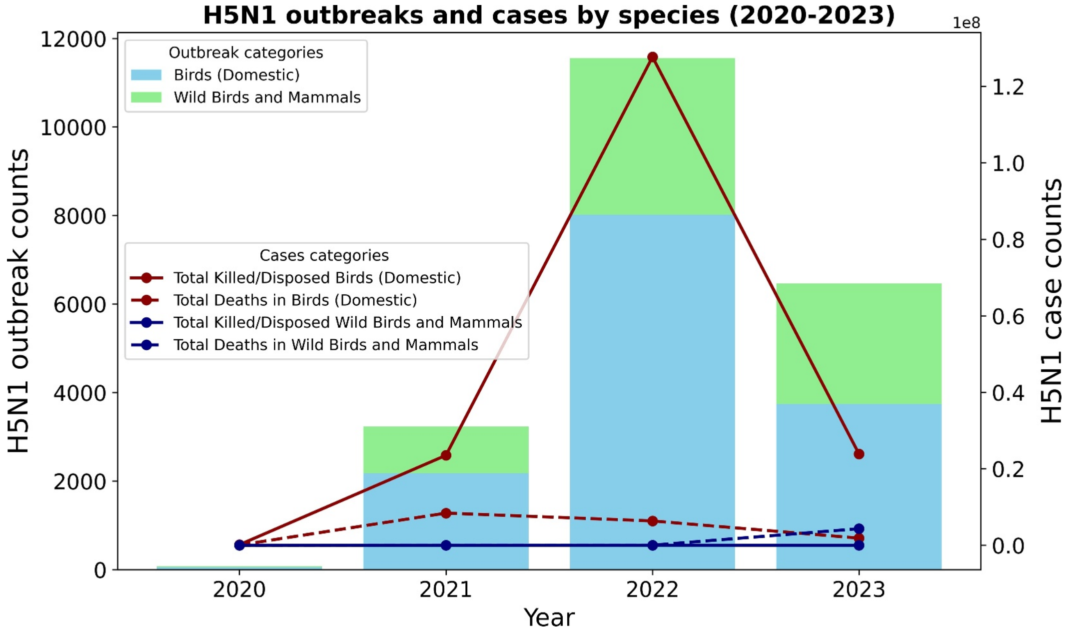

Figure 9. Frequency of H5N1 outbreaks and cases from 2020 to 2023 stacked by species.

virus and the risk of spill-over events to domestic birds and potentially humans. Although the frequency of H5N1 outbreaks and cases from 2020 to 2023 (Figure 9) does not explicitly discuss the zoonotic potential of AIV, yet the presence of the virus in both domestic and wildlife underlines the need for vigilance.

4.5. Leading Countries Affected by H5N1 Avian Influenza Outbreaks

Figure 10 offers a detailed portrayal of the prevalence of H5N1 outbreaks, delineating the distinction between domestic and wild avian populations. The graph indicates a significant skew toward domestic bird cases, with France, Germany, and the US emerging as the countries with the highest incidence of outbreaks. While France and Hungary report a higher prevalence of domestic bird cases, the Netherlands and Belgium show a relative

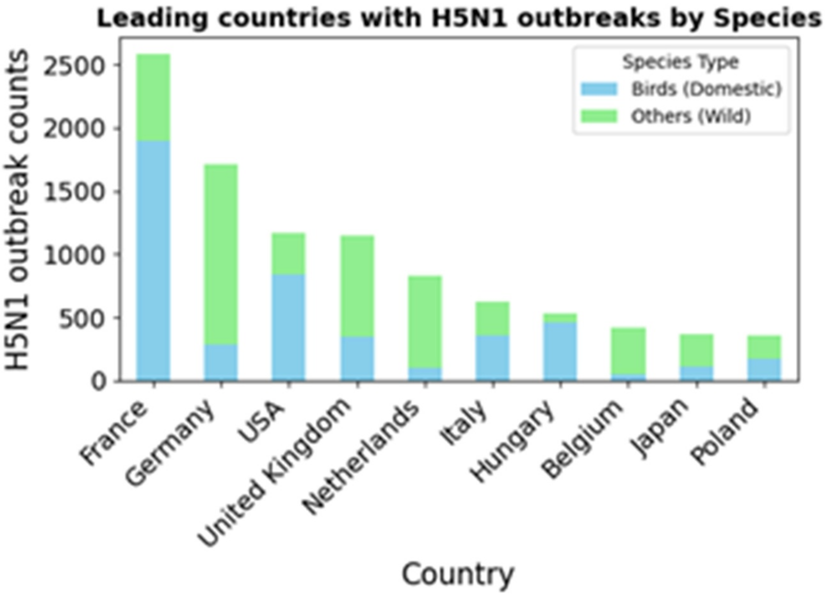

Figure 10. Countries with highest frequency of H5N1 outbreaks (2020–2023).

increase in wild bird cases. The absence of any country without reported cases in wild species signals an extensive environmental reach of the virus. It highlights the substantial role of natural bird migrations and international poultry trade in the transmission of AIV.

4.6. Hotspot Analysis

Table 1 summarizes the regions identified as hotspots and coldspots for H5N1 outbreaks across 11 kinds of bird families, highlighting the spatial patterns of disease distribution. Figure 11 displays the hotspots and coldspots for four major bird families that have been affected the most (Figure 1). Plots for other bird families can be referenced from the Supporting Information S1. This approach provides a strong framework for the identification of specific regions at higher risk for H5N1 outbreaks and upon which to further evaluate these patterns with targeted intervention studies and research into what is driving these patterns.

5. Discussion

The findings presented in this study shed light on the role of wild bird migration in the significant inter-continental spread of the H5N1 strain affecting wild birds, mammals, and domestic birds at a wide scale. These results hold significant implications for the potential mutation of the virus in human beings. By examining the migration routes of the wild birds along with the incidence of H5N1 especially clade 2.3.4.4b from 2020 to 2023, we were able to uncover the transmission of the virus from Europe to the American continent and parallelly from Europe to the African continent. In light of these results, several important points emerge for consideration.

In January 2020, AIV was predominantly observed in Asian countries, notably China and India. China, a key player in the poultry industry, exports poultry to several countries including Japan, Mongolia, Hong Kong, Cambodia, and Malaysia. Similarly, India engages in poultry exports to Maldives, Malaysia, Bhutan, Bahrain, Mauritania, and Comoros. The potential dissemination of AIV to Malaysia, Vietnam, and surrounding islands is speculated to be linked to the import of poultry from other Asian countries. As the northward migration of birds occurred in February and March 2020, AIV subsequently spread to Europe, with Denmark being an early affected country, and continued to propagate in neighboring nations.

In December 2020, during the southward migration of birds, a few cases of AIV began to emerge in Africa, specifically in the Mali region. This timeline highlights the dynamic nature of AIV spread, intricately connected with bird migration patterns and international poultry trade.

In March 2021, the northward migration facilitated the spread of AIV to several northern European countries, including Germany, the Netherlands, the UK, Hungary, Denmark, Poland, and Slovakia. By the end of 2021, the virus had become widespread across European nations. Notably, during the southward migration in late July, AIV extended its reach to Africa, affecting regions such as Mali and Nigeria.

The occurrence of AIV in South Africa from March to June 2021 appears to be unrelated to bird migration, given that this period corresponds to the northern hemisphere's breeding season when birds typically remain in the north. Instead, the introduction of AIV to South Africa is associated with the importation of poultry from Denmark, Ireland, and Spain.

Throughout the latter half of 2021, cases continued to proliferate in Europe, Africa, and Asia. In October, a single dead bird was discovered in Iceland, signaling the presence of the virus in that region. Subsequently, in December, a dead owl was found on the eastern coast of Canada, indicating the initiation of AIV spread to the Americas.

Between February and July 2022, a substantial spread of AIV occurred from the east coast to the west coast of the US and extended into Canada. In October, AIV cases began to emerge in Panama and Mexico, aligning with the southward migration period. By the beginning of November, the virus had extended its reach to Peru, manifesting along the entire coast. The mid-November to December timeframe witnessed the further spread of AIV to Chile, encompassing the entire coastal region. These temporal and geographical patterns underscore the dynamic nature of AIV dissemination, influenced by migratory patterns and regional factors.

In January and February 2023, the westward spread of AIV to the coastal regions of South Africa, particularly in Chile, is notable, and the infections in this region appear to primarily affect wild mammals, possibly seals. By late February, a sporadic increase in AIV cases in Argentina was predominantly observed in domestic poultry. However, as the situation progressed, cases in Uruguay and Brazil during May were noted to predominantly

Table 1
Summary of H5N1 Outbreak Hotspot and Coldspot Analysis Across 11 Bird Families

Bird family	Hotspots predictions	Coldspots predictions
Accipitriformes	Concentrated in Central Europe; regions particularly vulnerable to H5N1 outbreaks	Few coldspots, mainly in Western Europe; possibly areas with effective control measures or lower bird densities
Anseriformes	Widespread across North America, Europe, and Asia; linked to migratory patterns and habitat preferences	Scattered globally, especially in Africa and South America; regions with fewer-than-expected outbreaks
Charadriiformes	Northern and Central Europe; likely related to coastal and wetland habitats	Mainly in Europe; possible lower bird densities or effective interventions
Ciconiiformes	Limited hotspots in Europe and Asia; sporadic outbreaks	Minimal coldspots; outbreaks are less concentrated, suggesting sporadic distribution
Columbiformes	Hotspots in Europe; are linked to urban environments where pigeons and doves are prevalent	Coldspots in Europe; possibly due to successful local control efforts
Galliformes	Central Europe; high concentration likely due to poultry farming activities	Very few coldspots; intense concentration of outbreaks in hotspot regions
Gruiformes	Isolated hotspots in Asia and Europe; limited significant vulnerability	Scattered coldspots; are regions with fewer outbreaks, possibly due to lower densities or different ecological behaviors
Passeriformes	Isolated hotspots in Asia and Europe; limited significant vulnerability	Dispersed coldspots; areas where outbreaks are lower than expected
Pelecaniformes	Europe and parts of Asia; are specific regions with significant vulnerability	Scattered coldspots; possibly related to lower bird densities or protective environmental factors
Podicipediformes	Few hotspots in Europe; with limited but significant vulnerability in certain areas	Minimal coldspots; overall low incidence of outbreaks in this family
Strigiformes	Concentrated in parts of America; suggests higher susceptibility to H5N1 in these regions	No coldspots were identified, indicating that other regions have a balanced or expected outbreak rate

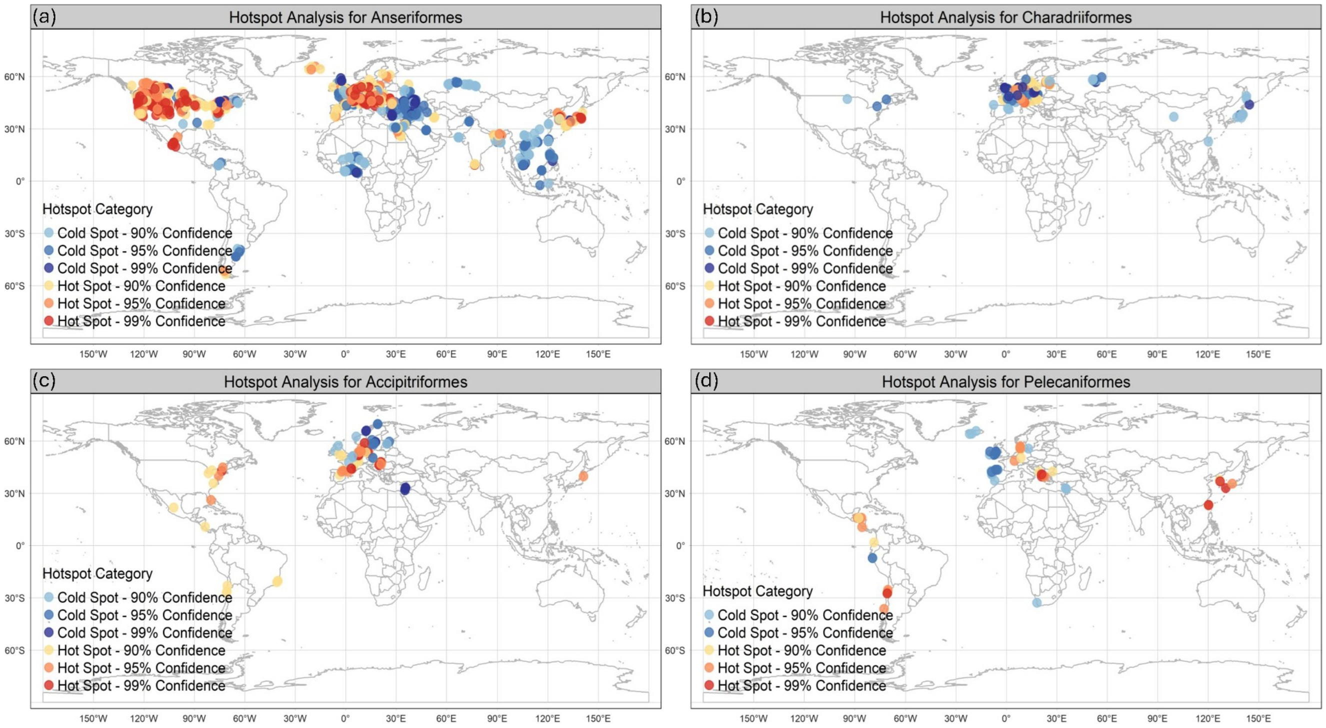

Figure 11. Hotspot Analysis for predicting H5N1 outbreaks per bird family (a) Anseriformes, (b) Charadriiformes, (c) Accipitriformes, and (d) Pelecaniformes.

involve wild birds and mammals. These observations highlight the diverse patterns of AIV spread, with variations in affected species and modes of transmission in different geographic regions.

Analysis from 2005 to 2023 indicated a cyclic occurrence of the H5N1 every 5 years. However, a noteworthy deviation from this established pattern has become apparent in the latest outbreak since 2020. The ecological dynamics of the virus seem to have undergone a significant shift, manifesting in an unprecedented surge in cases compared to previous outbreaks. What distinguishes this event is the simultaneous and extensive infection of poultry, birds, and mammals during the same season—a phenomenon not witnessed in prior instances.

Overall hotspot analysis confirms that the rate of H5N1 infection has been declining in the Asian countries as shown by the consistent coldspots in these regions across all bird families, while the hotspots have now shifted to the UK and USA regions.

The unprecedented scale and simultaneous infection across multiple species raise concerns about the potential threats to human health, especially in the upcoming years, if not months. The looming increase in bird migrations to the south adds a layer of complexity and urgency to the situation. As we navigate this evolving landscape, it becomes imperative to closely monitor and comprehend the altered dynamics of the virus to implement effective strategies for mitigating the risks associated with human infections.

6. Concluding Remarks

In this study, we tracked the movement of some wild birds according to their seasonal migration along with the incidence of H5N1. While the spread patterns revealed that the AIV had started in Asian countries, it is not clear how it spread from Asia to Europe because, with the birds we analyzed, it was unable to find a flyway from Asia to Europe. However, every spread after the first incidence of AIV in Europe can be correlated with the seasonal migration of birds from one country to the other. Europe to Greenland to North America to South America can be established with different wild birds along with the spread from Europe to Africa.

By tracking the migratory pathways of wild birds during their migration periods and correlating them with incidences of AIV outbreaks, this study has provided some insights into the patterns of AIV spread. However, there are several avenues for further research and enhancement of the existing framework.

First, the inclusion of detailed spatial data on poultry farm locations and poultry networks will enable a more comprehensive understanding of the interactions between wild birds and domestic poultry in the transmission of AIV. By analyzing the proximity of migratory bird habitats to poultry farms and tracing potential transmission pathways, we can better elucidate the mechanisms driving AIV transmission dynamics.

Furthermore, the potential for mapping out African avian outbreaks in greater detail presents an important opportunity for addressing the gaps in AIV surveillance in the region. Given the scarcity and delay in reporting AIV outbreaks in many African countries, leveraging geospatial analysis to identify high-risk areas and predict outbreak hotspots can significantly enhance early detection and response efforts.

Moreover, incorporating advanced geospatial modeling techniques, such as spatial clustering analysis and predictive modeling, can further refine our understanding of the spatial-temporal patterns of AIV transmission. By integrating diverse data sets, including environmental factors, land use patterns, and human population density, we can develop more accurate predictive models to anticipate future outbreaks and inform targeted intervention strategies. Overall, by leveraging geospatial technologies and interdisciplinary approaches, we can enhance surveillance, prediction, and control efforts to mitigate the impact of AIV on both animal and human health.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

The data collected for avian influenza is publicly available through the World Animal Health Information System (WAHIS) at https://wahis.woah.org/#/event-management. Poultry trade data is available from the International Poultry Council (IPC) at https://internationalpoultrycouncil.org/resources/.

Acknowledgments
The first author would like to acknowledge the support through a Tuition Fee Scholarship Award from the University of New South Wales. Open access publishing facilitated by University of New South Wales, as part of the Wiley - University of New South Wales agreement via the Council of Australian University Librarians.

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