Mapping Mechanistic Modeling of Highly Pathogenic Avian Influenza Across Migratory Flyways: A Systematic Review

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Abstract

Highly pathogenic avian influenza (HPAI) viruses, particularly H5N1 clade 2.3.4.4b, continue to spread globally via wild migratory birds along defined flyway corridors. Mechanistic models are essential tools for understanding HPAI transmission dynamics in flyway systems. Yet the geographic distribution of such modeling efforts across migratory flyways remains unknown. To inform the global response to HPAI, we conducted a PRISMA-compliant systematic review of published mechanistic and mathematical models of HPAI that explicitly incorporate migratory wild bird populations, organizing findings within a flyway-stratified framework. A search of PubMed, Scopus, Web of Science, and Embase yielded 582 records, of which 30 met inclusion criteria: 20 HPAI-specific models (H5N1, H5N8, H5N6, multiple HPAI subtypes) and 10 general avian influenza virus (AIV) models or pre-2016 H7N9 studies retained for their transmission dynamics relevance. Included studies spanned 2010–2025, with a marked surge in 2025 following worldwide transmission of HPAI in the early 2020s. The East Asian–Australasian Flyway (EAAF) dominated modeling effort (35.6% of studies), followed by the East Atlantic (15%), Central Asian (12.2%), Mediterranean–Black Sea (11.7%), and Americas flyways (10%). American (10%), European (27%) and African flyways (2.2%) were underrepresented, despite carrying millions of migratory waterfowl annually and experiencing unprecedented HPAI activity since 2020. Compartmental ordinary differential equation (ODE) models were the most common framework (33.3%) used across the included studies, followed by agent-based and spatial models (20% each). H5N1 dominated subtype coverage (53.3%). We identified several recurring methodological simplifications: models typically assumed homogeneous mixing within populations, rarely linked wild bird reservoirs to domestic livestock such as poultry and human spillover in full transmission chains, and underutilized available empirical tracking data. Our findings reveal a systematic geographic asymmetry in HPAI mechanistic modeling that misaligns with current global outbreak distributions, with direct implications for early warning system development and international surveillance coordination.

Keywords:
Mechanistic models; Highly pathogenic avian influenza (HPAI); Wild birds; Migratory flyways; Zoonotic spillover; One Health

1. Introduction

Highly pathogenic avian influenza (HPAI), caused by strains of influenza A virus such as H5N1, H5N8, H5N6, and H7N9, poses a sustained threat to poultry industries, economies, and public health globally [1–3]. Since the first confirmed human H5N1 case in Hong Kong in 1997 [4], sporadic zoonotic spillover events have occurred across

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Asia, Europe, Africa, and North America,with cumulative case fatality rates approaching 50% [5]. The ongoing global spread of clade 2.3.4.4b H5N1 since 2021, including incursions into mammalian species and dairy cattle, has further intensified pandemic concern [6, 7].

Wild migratory waterfowl are natural reservoirs for avian influenza virus (AIV) and can contribute to long-distance spread of some HPAI lineages across national borders and between continents along structured migratory corridors known as flyways [8, 9]. Eight major flyways are recognized worldwide [10], each representing a distinct transmission corridor with characteristic species assemblages, stopover ecologies, and interfaces with domestic livestock systems. HPAI transmission dynamics vary substantially between flyways due to differences in migration phenology, contact patterns among co-migrating species, local environmental conditions, and spatial overlap with livestock (such as poultry and dairy cattle) production [11–14]. Flyways therefore represent the most ecologically appropriate spatial unit for understanding and anticipating HPAI dispersal at regional and global scales.

Mathematical and mechanistic models including compartmental ordinary/partial differential equation (ODE/PDE) frameworks, stochastic models, agent/ individual-based and spatial modeling approaches are essential tools for characterizing HPAI transmission dynamics, estimating epidemiological parameters, and evaluating intervention strategies [15, 16]. Recent systematic reviews reported in the literature such as [17, 18] identified mathematical, statistical, and machine learning models of avian influenza dynamics, highlighting important gaps in validation practices, control and data integration. However, these reviews organized findings by model type, control and application rather than by geographic or ecological context. Consequently, it remains unknown which flyways are well-characterized mechanistically, which are understudied, and what the implications of this uneven distribution are for global HPAI preparedness.

Given the flyway-specific transmission dynamics, effective pandemic preparedness requires mechanistic modeling frameworks tailored to each major flyway. Yet the geographic distribution of HPAI modeling efforts across flyways (and which flyways remain understudied) remains unknown. This systematic review addresses that gap by conducting a comprehensive synthesis of published mechanistic models of HPAI that incorporate migratory or wild bird populations, organized within a flyway-stratified framework. Specifically, we aim to: (i) systematically identify relevant mechanistic modeling studies; (ii) classify studies by migratory flyway using BirdLife International boundary definitions [19] (as shown in Fig. 2); (iii) quantify the geographic, temporal, and methodological distribution of modeling effort; and (iv) identify understudied flyways and priority areas for future work. The review follows the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines [20, 21].

2. Methods

2.1. Protocol and registration

This systematic review was conducted and reported in accordance with the PRISMA [20] guidelines. The review protocol and all supporting materials were registered on the Open Science Framework (OSF) (`10.17605/OSF.IO/ECM2Z`). The registered protocol documents the complete search strategy, inclusion and exclusion criteria, data extraction framework, and flyway classification protocol.

2.2. Search strategy and databases

A systematic literature search was conducted across four electronic databases: PubMed, Scopus, Web of Science, and Embase. These databases were selected for their complementary coverage of biomedical, ecological, computational, and veterinary research. The search was conducted on March 03, 2026 with no restriction on publication date.

The search string was structured around three conceptual blocks combined with Boolean `AND` operators: (i) HPAI virus terms, (ii) mechanistic modeling terms, and (iii) migratory bird and flyway terms. The full search string applied across all databases is provided in Supplementary Table S1. We adapted our syntax for specific databases like Scopus, which limits string length. In those cases, we ran the search in batches and then joined the results using Scopus's combine feature.

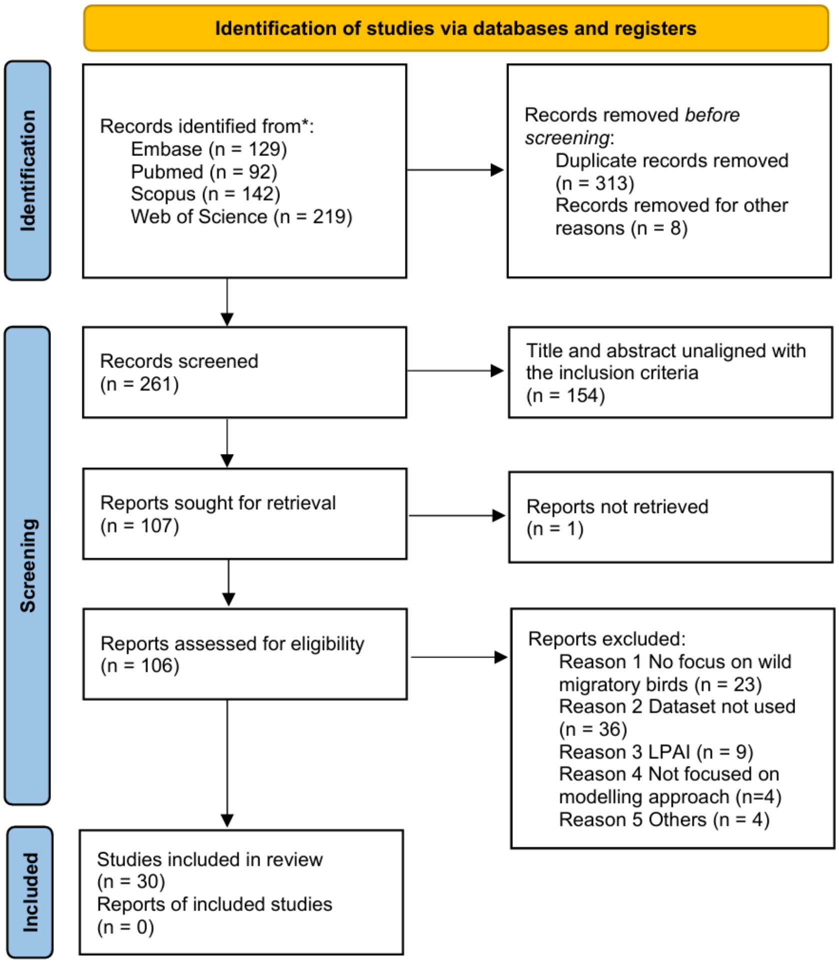


Figure 1: Flowchart of PRISMA.

2.3. *Study selection process*

Screening was conducted in two sequential stages using Rayyan [22]. Title and abstract screening (Stage 1) was performed independently by two reviewers (Z.A. and N.C.S.), with disagreements resolved through discussion. In Stage 1, all titles and abstracts were screened against the eligibility criteria, with records classified as include, exclude, or uncertain. In Stage 2, full texts of all records passing initial screening were retrieved and assessed for eligibility. Reasons for exclusion at the full-text stage were documented and are reported in the PRISMA flow diagram Fig. 1. Full text of all studies was retrieved via institutional access (thanks to the University of Naples and University of Campania). Only one study was not retrieved due to being inaccessible; that study was therefore excluded from our analysis.

2.4. *Eligibility criteria*

Studies were included if they employed a mathematical or mechanistic modeling framework to analyze HPAI (subtypes H5N1, H5N8, H5N6, H5N2, H7N9) or general avian influenza virus (AIV) not exclusively focused on low-pathogenic avian influenza (LPAI). Eligible modeling approaches encompassed ordinary and partial differential equation (ODE/PDE) models, stochastic models, metapopulation or patch models, network models, agent-based models, and spatial or statistical models that explicitly incorporate migratory bird movements.

Critically, studies were required to explicitly incorporate migratory birds, wild bird populations, or flyway-relevant movement as a *core component* of the modeled system, with a defined geographic study area (at any spatial scale from

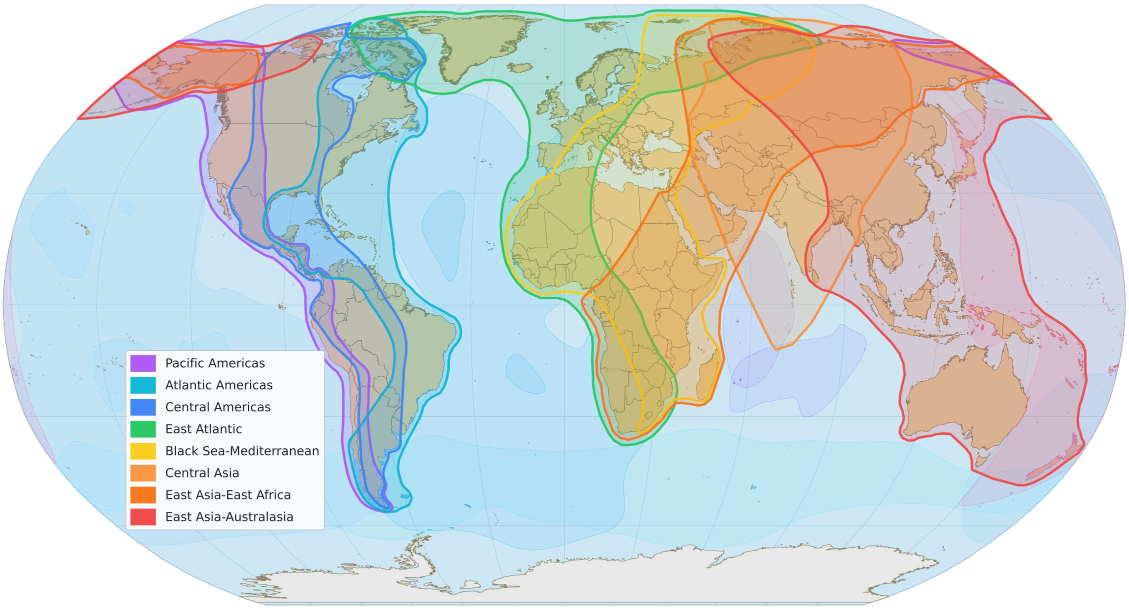


Figure 2: Global map of bird migration flyways, illustrating the major routes used by migratory birds across continents. Data sourced from BirdLife International DataZone [19]

local to global). We included studies that modeled transmission across multiple host populations (wild birds, domestic poultry, livestock, humans) as long as wild bird movement or migratory connectivity was explicitly represented. We excluded studies that modeled only within-farm or within-flock poultry transmission without wild bird or migratory connectivity components, as these represent a distinct transmission pathway (e.g., poultry trade networks) operating at different spatial and temporal scales from flyway-mediated dispersal. Additionally, studies must have been written in English and published in peer-reviewed journals or conference proceedings.

Studies were excluded if they: (i) employed purely simulation-based approaches without explicitly incorporating empirical data; (ii) focused exclusively on LPAI with no HPAI component or potential for mutation to HPAI; (iii) did not specify a defined geographic study area; or (iv) were review articles, meta-analyses, editorials, commentaries, opinion pieces, or conference abstracts without accompanying full-text publications.

2.5. *Data extraction framework*

A standardized data extraction framework was developed to systematically capture key information from included studies. Data were extracted using a predefined template covering seven core domains: (i) study identification (author, year), (ii) model type and mathematical framework, (iii) HPAI subtype(s) investigated, (iv) country or region of focus, (v) flyway assignment according to the classification protocol described in Section 2.6, (vi) data type utilized for model parameterization, and (vii) population type modeled (wild birds, domestic poultry, or mixed systems). All extracted data are presented in Table 5.

2.6. *Flyway classification protocol*

Migratory flyways represent ecologically appropriate spatial units for characterizing HPAI transmission because host movement patterns, species composition, stopover ecology, and environmental conditions, which all influence transmission dynamics, vary substantially between flyways [11–14]. Assignment of included studies to migratory flyways constitutes the primary organizational novelty of this review and therefore required a transparent, reproducible classification protocol defined a priori.

We adopted the eight major flyway designations used in our spatial reference map as shown in Fig. 2. The eight flyways are: (i) East Asian–Australasian, (ii) Central Asian, (iii) East Atlantic, (iv) Mediterranean–Black Sea, (v)

East African - East Asian, (vi) Central Americas (including the Mississippi), (vii) Pacific Americas, and (viii) Atlantic Americas. Geographic boundary shapefiles were obtained from the BirdLife International DataZone [10] (Fig. 2) and used as the reference layer for all assignments.

For studies assigned to multiple flyways based on geographic overlap, fractional weighting was applied. Studies explicitly naming a single flyway received a full count (weight = 1.0) for that flyway. Studies whose study area (geographic region analyzed in the modeling framework) intersected multiple flyways without explicit flyway designation received fractional counts proportional to the number of flyways spanned (e.g., a study covering a country intersecting three flyways = 0.33 count in each) as shown in Table 1. If the geographic scope was ambiguous or insufficiently described to permit unambiguous assignment, for example, described only at the continental or global level without further spatial delineation, the study was classified as unassignable and reported transparently in the results.This approach ensures that all relevant evidence is captured for each flyway without artificially inflating study counts. By weighting the assignments, the sum of flyway counts approximates the total number of unique studies (n = 30). Consequently, percentages represent the proportion of these 30 unique studies found within each flyway.

3. Results

3.1. Search results and study selection

The PRISMA flow diagram is presented in Fig. 1. We searched four databases (Embase, PubMed, Scopus, Web of Science) and identified 582 records. After removing 313 duplicates and 8 ineligible record types (reviews, meta-analyses, editorials, commentaries, and conference abstracts), 261 records underwent title and abstract screening. We excluded 154 records that did not meet our predefined inclusion criteria; 106 records were considered for full-text assessment.

We excluded 76 studies at full-text review: 36 lacked empirical data parameterization, 23 did not include wild bird populations, 9 focused exclusively on LPAI rather than HPAI, 4 were not modeling studies, and 4 were excluded for other reasons (wrong disease or population type). A total of 30 studies met all inclusion criteria and were included in the final synthesis.

3.2. Temporal and geographic distribution

3.2.1. Publication trends over time

During initial search, no temporal restrictions were applied, which returned publications spanning 2000 to 2025. However, after applying inclusion and exclusion criteria, all 30 retained studies were published between 2010 and 2025, indicating that earlier publications either did not meet eligibility requirements or that mechanistic modeling of HPAI in migratory bird systems emerged as a distinct research focus around 2010. Annual publication frequency remained modest through 2020, ranging from 1 to 3 studies per year (Fig. 3d). A marked surge occurred in 2025, when 7 studies (representing 23.3% of the total included literature) were published.

3.2.2. Geographic distribution by Country

The geographic distribution of included studies reflected major HPAI-affected regions and active surveillance networks. However, the identification of these as "major HPAI-affected regions" may itself be biased by the concentration of modeling research in those same areas (see Section 4.3 for discussion of detection bias and surveillance heterogeneity). China was the most frequent geographic focus, appearing in seven studies total. Five of these (16.6%) focused exclusively on Chinese regions or populations, while two others included China as part of a regional or flyway-scale analysis. The United States was the focus of only one study (3.3%), while North America as a whole (encompassing Canada and the United States) was addressed by a further two studies (6.6%). The Netherlands, Australia, and India each contributed two studies (6.6% each). Single studies were identified for Spain, Germany, Croatia, Mongolia, Bangladesh, Nigeria, and Lake Constance (Europe), each representing approximately 3.3% of the included literature. The geographical distibution of the studies conducted is given in Supplementary Fig. S1.

Flyway-scale or multi-country studies constituted a substantial proportion of the synthesis. Three studies adopted a global scope (10%), one study covered Europe at the continental level (3.3%), and one study was explicitly multi-country (3.3%). Three studies focused specifically on the East Asian–Australasian Flyway (EAAF) or the broader associated region (10%), and one study addressed the Central Asian Flyway (CAF) (3.3%).

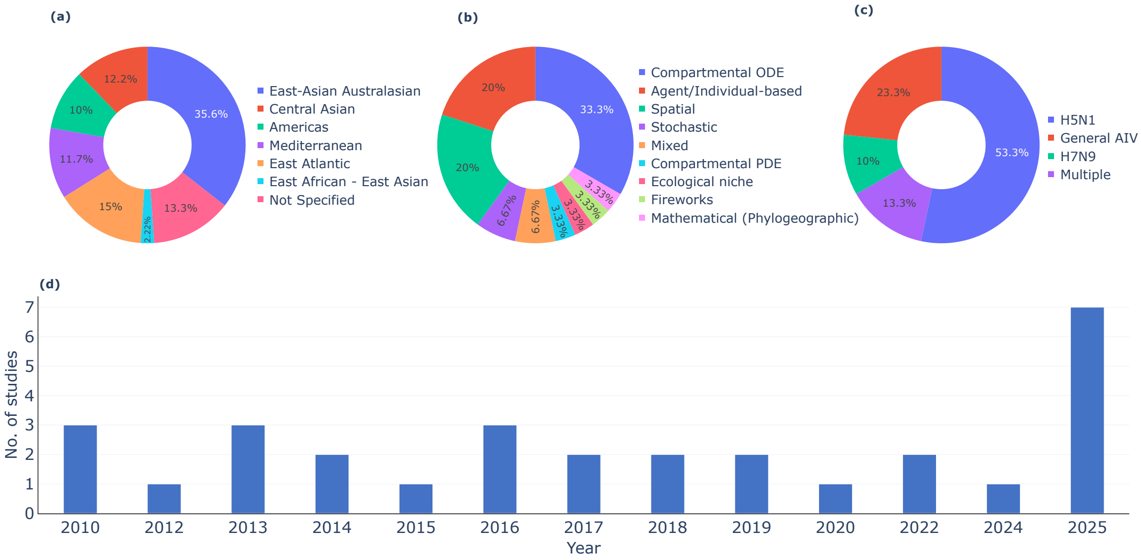


Figure 3: Characteristics of included HPAI modeling studies (n=30). (a) Distribution by flyway (flyway-weighted percentages; see Section 2.6) (b) Distribution by modeling framework (c) Distribution by HPAI subtype investigated (d) Temporal distribution by publication year (2010–2025).

Table 1: Flyway assignments and fractional weightings for all included studies (n=30). See Section 2.6 for complete classification protocol.

Study	**Country/ Region**	**Flyway**	**Flyway Weightage**
Llanos-Soto et al. 2025 [23]	Croatia	Mediterranean	1.0
Takekawa et al. 2025 [24]	Mongolia	Central Asia + East-Asia Australasia	0.5 each
Yin et al. 2025 [11]	East Asian-Australasian region	East Asia-Australasia	1.0
Castonguay et al. 2025 [25]	Bangladesh	East Asia-Australasia	1.0
Mursel et al. 2025 [26]	USA	Pacific + Central + Atlantic	0.33 each
Chanda et al. 2025 [27]	India (Kerala)	Central Asia	1.0
Ewing and Bouwhuis 2025 [28]	Germany	East Atlantic	1.0
McDuie et al. 2024 [29]	North America	Pacific + Central + Atlantic	0.33 each
Schreuder et al. 2022 [30]	Netherlands	East Atlantic	1.0
Yin et al. 2022 [31]	Multiple along the flyway	East Asia-Australasia	1.0
Pereira et al. 2020 [32]	Europe in general	Mediterranean + East Atlantic	0.5 each
Barnes et al. 2019 [33]	Australia	East Asia-Australasia	1.0
Rao 2019 [34]	Global	not specified	1.0
Lisovski et al. 2018 [35]	Netherlands	East Atlantic	1.0
Endo and Nishiura 2018 [36]	Flyway scale	East Asia-Australasia	1.0
Zhang et al. 2017 [37]	China	East Asia-Australasia	1.0
Fourment et al. 2017 [12]	USA and Canada	Pacific + Central + Atlantic	0.33 each
Prosser et al. 2016 [38]	China	Central Asia + East-Asia Australasia + East Asia - East Africa	0.33 each
Xu et al. 2016 [39]	China	East Asia-Australasia	1.0
Zhang 2016 [40]	China	East Asia-Australasia	1.0
Brown et al. 2015 [41]	Nigeria	Mediterranean + East Atlantic	0.5 each
Zhang et al. 2014 [42]	China	East Asia-Australasia	1.0
Rao 2014 [43]	Global	not specified	1.0
Pandit et al. 2013 [44]	India	Central Asia + East Asia-Australasia	0.5 each
Tuncer & Martcheva 2013 [45]	Global (with focus on Indonesia, Egypt, Vietnam, China)	not specified	1.0
Prosser et al. 2013 [46]	China	Central Asia + East-Asia Australasia + East Africa - East Asia	0.33 each
Alba et al. 2012 [47]	Spain (Catalonia)	Mediterranean	1.0
Penny et al. 2010 [48]	Lake Constance (Europe)	East Atlantic + Mediterranean	0.5 each
Henaux et al. 2010 [49]	Not country-specific. Field prevalence data from North America (Canada, USA) and Europe.	not specified	1.0
Bourouiba et al. 2010 [50]	Mongolia (Primary Breeding) → China (Stopovers & Secondary Breeding, e.g., Qinghai Lake/Tibet) → Himalayas Crossing → India (Wintering)	Central Asia	1.0

Table 2: Distribution of HPAI subtypes modeled by major flyway. Numbers represent number of studies (or flyway-weighted count in parentheses). Multiple/mixed contains those having multiple HPAI strains or a mix of LPAI and HPAI, including mutations. Total is the sum of flyway-weighted.

Flyway	**H5N1**	**H7N9**	**Multiple/Mixed**	**General AIV**	**Total**
East Asian–Australasian	5 (2.67)	3 (3)	2 (2)	3 (3)	10.67
Central Asian	5 (2.67)	0	1 (1)	0	3.67
East Atlantic	4 (2.5)	0	1 (1)	1 (1)	4.5
Mediterranean–Black Sea	4 (2.5)	0	1 (1)	0	3.5
Americas	2 (2)	0	0	1 (1)	3.0
East African–East Asian	2 (0.67)	0	0	0	0.67
Not Specified	3 (3)	0	0	1 (1)	4.0
Total	**16**	**3**	**4**	**7**	**30**

3.2.3. Distribution by model types

Compartmental ODE models (SIR, SEIR, SIS) were the most frequently employed modeling approach, accounting for 10 studies (33.3%). It is worth noting here that the compartmental models were considered on the basis of linking wild birds with the secondary or tertiary reservoirs, such as livestock and humans, or those considering transmission among wild bird species only. Agent-based or individual-based models (ABM/IBM) and spatial models were used in six studies each (20% each). Stochastic models (e.g., Gillespie simulations, stochastic branching processes) were employed in two studies (6.6%). Ecological niche models, fireworks models, and partial differential equation (PDE) models each appeared in one study (3.3% each). Notably, two studies (6.6%) combined two or more modeling approaches (e.g., ABM with SIR, or spatial or stochastic frameworks with compartmental dynamics). The overall distribution of the model types identified is shown in Fig. 3b.

3.2.4. HPAI subtypes and geographic distribution

More than half of all studies focused on HPAI H5N1 (n=16, 53.3%), distributed across all flyways but concentrated in Asian systems. Seven studies examined general avian influenza virus (AIV) without specifying pathotype (23.3%), scattered across multiple flyways. Four studies investigated multiple or mixed HPAI subtypes (13.3%), distributed across Asian and European flyways. Three studies focused exclusively on H7N9 (10%), all in the East Asian–Australasian Flyway (reflecting the subtype's regional zoonotic history in China); these studies predate H7N9's 2016 transition to high pathogenicity [51, 52] and model LPAI H7N9 transmission, but were retained for their cross-species spillover relevance. Notably, H5N8 and H5N6, despite global distribution since 2016, are underrepresented relative to their pandemic relevance. The distribution of subtypes by flyway is detailed in Table 2, with overall subtype proportions shown in Figure 3c.

3.3. Flyway-stratified distribution

The distribution of included studies across major migratory flyways was highly asymmetric (Fig. 3a, Table 3). Applying the fractional weighting methodology described in Section 2.6 and Table 1, the East Asian–Australasian Flyway (EAAF) accounted for the largest proportion of modeling effort (35.6% of total studies). This includes nine studies that explicitly identified the EAAF as their study system, plus fractional contributions from studies covering countries or regions that intersect this flyway but did not specify flyway boundaries.

The remaining flyways were considerably underrepresented. The East Atlantic Flyway accounted for 15.0% of studies, followed by Central Asian (12.2%), Mediterranean–Black Sea (11.7%), and the Americas flyways (10.0%). The East African–East Asian flyway received minimal research attention (2.2% of total). Four studies (13.3%) were classified as "Not specified" due to global scope or insufficient geographic detail to permit unambiguous flyway assignment.

3.3.1. East Asian–Australasian flyway

The East Asian–Australasian Flyway (EAAF) was the most intensively modeled corridor, accounting for 35.6% of total studies (flyway-weighted count: 10.67 studies; see Table 1 Section 2.6 for weighting protocol). This concentration reflects the flyway's role as the historical epicenter of HPAI H5N1 emergence and its continued importance as a

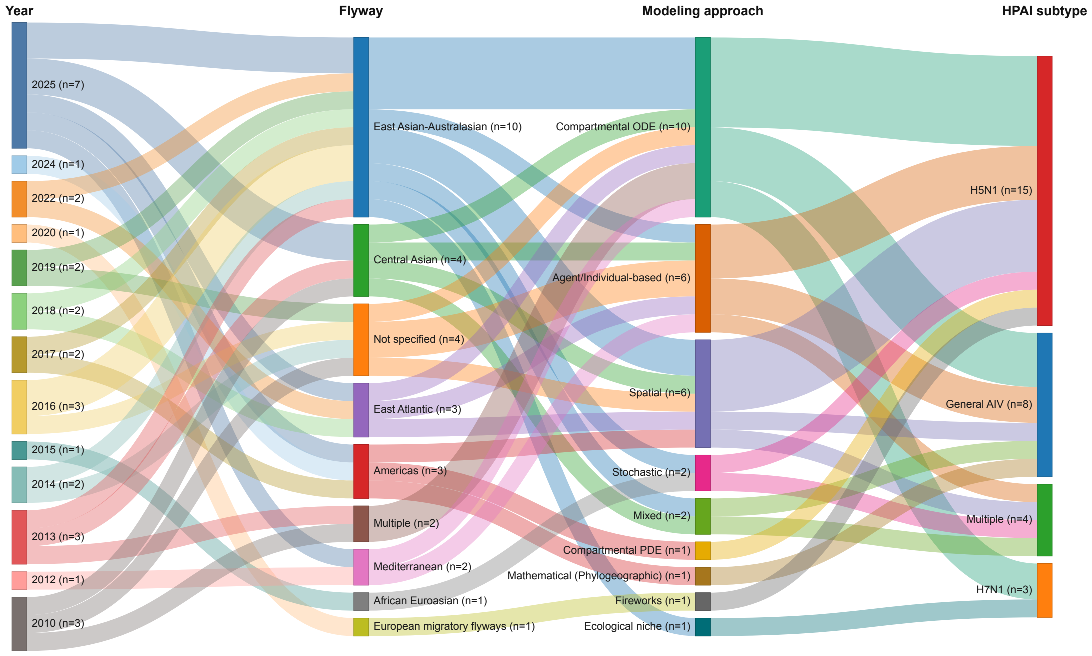


Figure 4: Information flow diagram (Sankey) showing relationships between publication year, flyway assignment, modeling approach, and HPAI subtype for 30 included studies. Flow width is proportional to the number of studies. Studies assigned to multiple flyways contribute fractionally to each relevant flyway (see Section 2.6 for weighting protocol).

high-risk transmission corridor connecting breeding grounds in Siberia and Mongolia to wintering areas in Southeast Asia and Australia.

Studies in this flyway employed diverse modeling approaches. Compartmental ODE models (SEIR, SI-SEIR) were most common, particularly for China-focused studies incorporating outbreak data, human case surveillance, and migration patterns [37, 40, 42]. Spatially explicit frameworks ranged from agent-based models parameterized with GPS telemetry [11] to multisite SIS models representing migration between discrete stopover regions [36]. Other approaches included spatial risk models [46], ecological niche models [39], stochastic branching processes [33], and mixed frameworks combining agent-based simulation with environmental transmission dynamics [31]. Notable examples include Castonguay et al. [25], who developed spatial models for Bangladesh integrating AIV occurrence data, climate projections, poultry census, and live bird market surveillance.

The distribution of EAAF modeling effort is shown in Figure 3a, with complete study listings in Table 3 and flyway weightings in Table 1. The relationships between publication year, flyway assignment, modeling approach, and HPAI subtype for all included studies (including EAAF studies) are illustrated in Figure 4.

3.3.2. Central Asian flyway

The Central Asian Flyway received moderate research attention, accounting for 12.2% of studies (flyway-weighted count: 3.67 studies). Modeling efforts concentrated on transmission dynamics along the Mongolia–China–India migratory corridor, where high-altitude migration across the Himalayas creates distinct epidemiological conditions.

Key contributions include Bourouiba et al. [50], who developed a spatial delay differential equation model parameterized with satellite tracking data to simulate bar-headed goose migration and HPAI spread between Mongolian breeding grounds and Indian wintering sites. Chanda et al. [27] employed Bayesian network modeling to link wetland irrigation patterns and duck-rice farming systems to recurrent H5N1 outbreaks in Kerala, India, identifying unique ecological drivers of persistence in this flyway. Agent-based approaches were used by Takekawa et al. [24] to model HPAI transmission in migratory swan goose flocks in Mongolia, while Pandit et al. [44] applied an SIR-SIC compartmental model to wild bird–domestic poultry interfaces in India.

Table 3: Distribution of modeling effort by flyway and representative total included studies (n = 30).

Flyway	**Contribution (n) %**	**References**
East Asian Australasian	(10.67) 35.6%	[11, 24, 25, 31, 33, 36–40, 42, 44, 46]
Central Asian	(3.67) 12.2%	[24, 27, 38, 44, 46, 50]
Mediterranean/Black Sea	(3.5) 11.7%	[23, 32, 41, 47, 48]
East Africa - East Asia	(0.67) 2.22%	[38, 46]
East Atlantic	(4.5) 15%	[28, 30, 35, 41, 47, 48]
Americas	(3) 10%	[12, 26, 29]
Not specified	(4) 13.3%	[34, 43, 45, 49]

3.3.3. East Atlantic flyway

The East Atlantic Flyway was represented by studies from northwestern Europe, particularly the Netherlands and Germany. Modeling efforts in this flyway emphasized local transmission dynamics at stopover sites, with a strong focus on mallards as the primary reservoir species [35]. Notable studies include a deterministic SIR and a stochastic SEIR ABM to estimate infection and recovery rates [28, 35]. A spatial model by Schreuder et al. [30] that accounts the wild birds outbreak and poultry outbreaks also fell within the same flyway.

3.3.4. Mediterranean–Black Sea flyway

The Mediterranean–Black Sea Flyway accounted for 11.7% of modeling effort (flyway-weighted count: 3.5 studies), comprising two studies that explicitly named this corridor plus fractional contributions from multi-flyway analyses. Llanos-Soto et al. [23] developed an SIR compartmental model fitted to outbreak data from wild migratory waterfowl in Croatia, examining spillover dynamics to backyard poultry farms during stopover periods. Alba et al. [47] applied agent-based modeling to AIV transmission in Catalonia, Spain, parameterized with population census data and prevalence estimates from wild bird surveillance. Pereira et al. [32] employed a fireworks spatiotemporal clustering algorithm to characterize HPAI outbreak patterns across multiple European flyways, including the Mediterranean–Black Sea corridor. Complete study listings are provided in Table 3.

3.3.5. East African - East Asian flyway

The East Africa - East Asian Flyway received no direct attention while only two studies fall in this flyway that meet our inclusion criteria which makes a total weighted contribution of only 2.22%. The studies contains spatial models by [38, 46] that consider China as their study region.

3.3.6. Americas flyways (Pacific, Central including Mississippi and Atlantic)

The Americas flyways were moderately represented in the literature, with studies distributed across the Pacific, Central, Mississippi, and Atlantic flyways. Key contributions include large-scale phylogeographic analyses demonstrating that within-flyway AIV migration rates were 4–13 times higher than between-flyway rates [12] and a spatiotemporal PDE model of SIR type that parameterized eBird abundance data of the wild mallard ducks [26]. McDuie et al. [29] developed a Contagion mathematical model that considered high-resolution tracking of 16 different wild waterfowl species across the American flyways.

3.4. Mathematical model structures used across flyways

3.4.1. Compartmental ODE/PDE models

Compartmental ODE models (SIR, SEIR, SIS, and their variants) were the most commonly employed framework, used in 10 out of 30 studies (i.e. 33.3%) [23, 35–37, 40, 42, 44, 45, 48, 49]. These models were typically used to estimate epidemiological parameters (e.g., transmission rates, recovery rates) from prevalence or outbreak data. Notable examples include Henaux et al. [49], who estimated infection and recovery rates for LPAI and HPAI in waterfowl using laboratory challenge data, and [37, 40, 42], who used a multi-host SEIR or SI-SEIR type models with a consideration of wild birds, poultry and human and their interactions for the spread of infection. Some of them extended the compartmental framework to include partial differential equations to model spatial diffusion such as [26].

Table 4: Distribution of modeling effort by flyway for HPAI only studies (n = 20).

Flyway	**Contribution (n) %**	**References**
East Asian Australasian	(4.67) 23.35%	[11, 24, 33, 38, 40, 44, 46]
Central Asian	(3.67) 18.35%	[24, 27, 38, 44, 46, 50]
Mediterranean/Black Sea	(2.5) 12.5%	[23, 32, 41, 48]
East Africa - East Asia	(0.67) 3.35%	[38, 46]
East Atlantic	(3.5) 17.5%	[28, 30, 41, 47, 48]
Americas	(2) 10%	[26, 29]
Not specified	(3) 15%	[34, 43, 45]

3.4.2. *Agent-based and stochastic models*

Agent/individual-based models (ABM/IBM) accounted for 20% of included studies. These models were particularly prevalent in flyway-scale analyses where individual variation in migration timing, stopover duration, and disease susceptibility was considered important. Examples include Yin et al. [11], who simulated HPAI transmission in migratory birds and assessed the impact of habitat loss on reassortment risk, and Takekawa et al. [24], who modeled HPAI H5N1 in Central Asian flyway with a focus on Mongolia considering the empirical field samplings of Swan Geese. Other ABM/IBM includes Rao et al. [34, 43] that developed an ABM of global perspective of H5N1 based on GIS data and WHO maps of wild birds and population estimates. Stochastic models were also used in two studies (6.6%) to capture demographic stochasticity in small populations [33, 41].

3.4.3. *Spatially continuous/landscape models*

Spatially continuous or landscape models were used in 20% of the included studies. These models simulated infection spread across continuous landscapes rather than discrete patches, typically integrating geographic information systems (GIS), remotely-sensed data, and empirical spatial heterogeneity. For instance, Prosser et al. [38, 46] developed risk models for H5N1 transmission at the wild bird–poultry interface in China. Similarly, Castonguay et al. [25] developed a spatial model of AIV in Bangladesh, integrating poultry census data, occurrence records, climate, and land cover. Other notable spatial frameworks include the work of Schreuder et al. [30] and McDuie et al. [29], as well as a delay differential equation model developed by Bourouiba et al. [50].

3.4.4. *Mixed and other types of models*

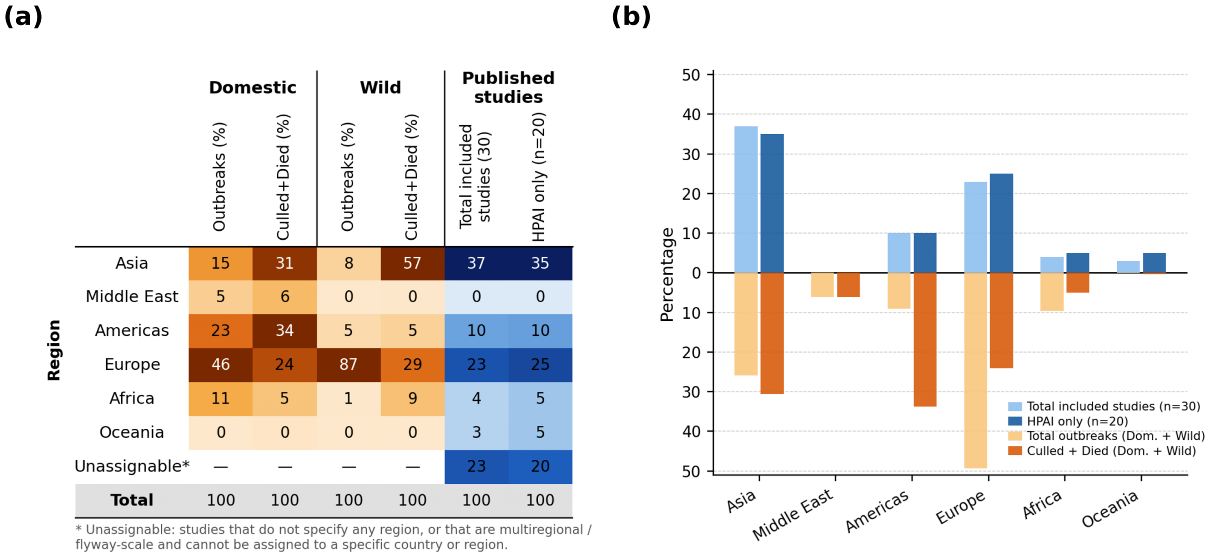
At least two models were employed in two studies (6.67%), primarily to represent different aspects of the disease. For example Chanda et al. [27] used a Bayesian Network model along with a stochastic PDE model in order to see that how infected migratory birds were the source of infection for the first few duck farms in the wetland areas and subsequent transmission was driven by shifting of ducks from one rice paddy field to other fields. Another mixed model by Yin et al. [31] involved using an ABM to simulate individual migration behavior of the Greater white-fronted goose in each network scenario along with a SIR model to simulate the AIV transmission in the population.

Other types of models includes a Ecological Niche model [39], a Mathematical-Phylogeographic model that considers Continuous-Time Markov Chain (CTMC) [12] and a fireworks like surveillance model [32].

3.5. *Primary data sources used*

Studies employed diverse data sources to parameterize bird movement and transmission dynamics, with considerable variation in spatial and temporal resolution. Outbreak surveillance and case data were most commonly used, providing empirical grounding for transmission rates, spillover events, and geographic spread patterns [23, 27, 40, 44]. GPS telemetry and satellite tracking provided high-resolution individual movement trajectories, including stopover locations, residence times, and flight paths, as demonstrated in studies of bar-headed geese crossing the Himalayas [50] and waterfowl in the East Asian–Australasian Flyway [11, 31].

Literature-derived parameters and prevalence data were frequently used when empirical tracking was unavailable, drawing on published estimates of movement ecology, transmission rates, and host susceptibility [33, 36, 49]. Citizen science platforms, particularly eBird, provided coarse-resolution abundance and distribution data for parameterizing population densities and seasonal occurrence [25, 26]. Remote sensing and land cover datasets informed habitat



(a)

Region	Domestic Outbreaks (%)	Domestic Culled+Died (%)	Wild Outbreaks (%)	Wild Culled+Died (%)	Published studies Total included studies (30)	Published studies HPAI only (n=20)
Asia	15	31	8	57	37	35
Middle East	5	6	0	0	0	0
Americas	23	34	5	5	10	10
Europe	46	24	87	29	23	25
Africa	11	5	1	9	4	5
Oceania	0	0	0	0	3	5
Unassignable*	—	—	—	—	23	20
Total	100	100	100	100	100	100

* Unassignable: studies that do not specify any region, or that are multiregional / flyway-scale and cannot be assigned to a specific country or region.

(b)

Figure 5: Regional distribution of avian influenza outbreak burden and published literature by host category. (a) Percentage of reported outbreaks and culled/died animals (domestic, wild) attributed to each region, expressed as a proportion of the global total per column. (b) Diverging bar chart comparing the regional share of published studies (above zero line; total included studies, $n = 30$; HPAI-only subset, $n = 20$) with the regional share of total reported outbreaks and culled/died animals (below zero line). Unassignable studies ($n = 7$ total; $n = 4$ HPAI only) that could not be attributed to a specific region are excluded from panel.

suitability and stopover site selection, with studies using wetland maps, rice paddy distributions, and vegetation indices to characterize transmission risk at landscape scales [31, 38, 46].

Environmental and climate data were incorporated in a subset of studies to parameterize migration timing and transmission suitability. Castonguay et al. [25] integrated climate projections with poultry distribution and land-use change, while Yin et al. [11, 31] incorporated vegetation indices and habitat quality metrics to assess stopover site attractiveness and bird aggregation risk. However, environmental driver integration remains limited despite clear importance for predicting both migration phenology and landscape-scale transmission dynamics.

Bird ringing data, particularly from European long-term monitoring programs, contributed migration timing and connectivity parameters [35], though use was limited compared to other data sources.

3.6. *Epidemiological parameters and model outputs*

Estimates of the basic reproduction number (R_0) were reported primarily in studies using compartmental models or next-generation matrix approaches. For HPAI in wild bird populations, R_0 estimates ranged from 1.1 to 3.7 across studies, with a median of approximately 1.7, including 3.7 (95% CI: 2.3–7.2) for H5N1 in common terns [28] and 1.1 (95% CI: 1.0–1.2) for general AIV in waterfowl along the East Asian–Australasian Flyway [36]. Transmission rates (β) were reported primarily in studies using experimental challenge designs or compartmental models fitted to outbreak data, with values varying widely depending on host species, setting, transmission mode, and pathogen strain; direct bird-to-bird transmission dominated for HPAI in dense breeding colonies [28]. For HPAI, infectious periods were shorter (typically 3–7 days) than for LPAI, reflecting higher mortality and faster disease progression. Mortality rates for HPAI in wild birds varied by species, age, and viral clade; in common terns, the probability of mortality for an infected bird was estimated at 0.26 (95% CI: 0.24–0.28) in 2022, declining to 0.14 (95% CI: 0.11–0.20) in 2023 [28]. Few studies directly estimated spillover probabilities from wild birds to poultry or humans, with exceptions including Zhang et al. [42], who estimated bird-to-human transmission rates for H7N9 in China, and Prosser et al. [46], who developed risk indices for poultry–wild bird transmission.

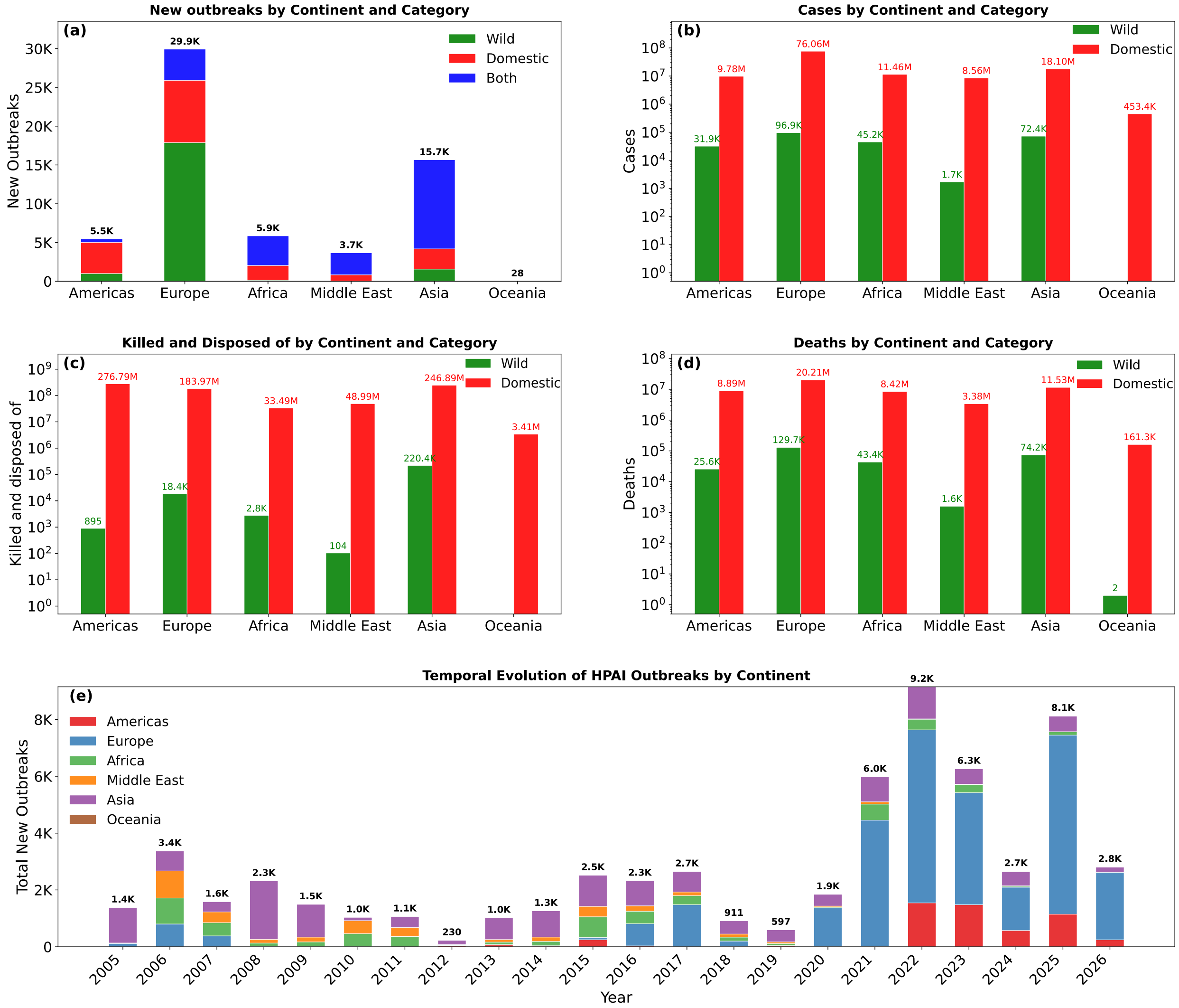


Figure 6: Global HPAI outbreak distribution by continent, 2005–2026 (data from World Organisation for Animal Health [53]). (a) Total outbreak events by continent and host category (wild birds, domestic poultry, both). (b) Total confirmed cases. (c) Total birds culled. (d) Total mortality. (e) Temporal evolution showing annual outbreak counts by continent. Middle East countries reclassified from Asia/Africa groupings to align with WOAH reporting conventions.

4. Discussion

4.1. Geographic asymmetry in HPAI modeling effort

A major finding of this systematic review is the asymmetry of mechanistic modeling effort across the wild bird migratory flyways as shown in Supplimentary Fig. S1. The East-Asian Australasian flyway, and the surrounding areas, remains the main focus of the modeling efforts. As per our inclusion criteria, we found over one-third (35.6%) of the studies focused on this flyway. Within this flyway, China remains the main focus with a major portion due to the availability of historical surveillance data from China and the persistence of HPAI H5N1 during the seasonal stopovers of the wild birds along the flyway [54, 55]. In contrast, the European migratory flyways (East Atlantic and Mediterranean–Black Sea, (Fig. S1) accounted for 26.7% of modeling efforts combined, substantially less than the East Asian–Australasian Flyway alone (35.6%), despite their ecological importance as routes for millions of waterfowl connecting Europe, Africa, and Asia [56, 57] and their sharply increased HPAI burden since 2020 [58, 59] (Figs. 6 and 7). The Americas flyways (Pacific, Atlantic, and Central, including the Mississippi) occupied an intermediate position concentrated on the USA and Canada while the East African - East Asian flyway was the most neglected flyway in the included literature.

4.2. *Sensitivity analysis - HPAI only vs. total included studies*

To assess whether the inclusion of general AIV and pre-2016 LPAI H7N9 studies influenced our primary findings, we conducted a sensitivity analysis restricting the dataset to HPAI-specific models only ($n = 20$).

Using fractional weighting (Section 2.6), the East Asian–Australasian Flyway accounted for 23.35% of HPAI-specific studies (4.67 weighted studies), followed by Central Asian (18.35%, 3.67 studies), East Atlantic (17.5%, 3.5 studies), Mediterranean–Black Sea (12.5%, 2.5 studies), Americas (10.0%, 2.0 studies), Not Specified (15.0%, 3.0 studies), and East African–East Asian (3.35%, 0.67 studies).

When aggregated by continental region, Asian flyways collectively accounted for 45.05% of HPAI-specific modeling (East Asian–Australasian 23.35% + Central Asian 18.35% + East African–East Asian 3.35%), compared to 30.0% for European flyways (East Atlantic 17.5% + Mediterranean 12.5%) and 10.0% for the Americas. This pattern is consistent with the full dataset, where Asian flyways accounted for 47.89% (East Asian–Australasian 35.6% + Central Asian 12.2% + East African–East Asian 2.2%), European flyways 26.7%, and Americas 10.0%. The flyway contribution for HPAI specific studies are given in Table 4.

4.3. *Geographical gap: historical burden vs. current risk*

The geographic asymmetry in HPAI modeling effort reflects historical detected outbreak patterns rather than current epidemiological risk. The reported distribution is subject to geographic heterogeneity in surveillance capacity: Asia has maintained intensive surveillance since H5N1 emergence in 1997, while Europe and the Americas intensified outbreak detection only after 2020 [60], and African regions likely experience substantial underdetection due to limited infrastructure [61, 62]. Despite these detection biases, the documented outbreak patterns provide the best available evidence of relative regional disease burden, and the divergence between modeling effort and detected outbreak events remains substantial even accounting for surveillance heterogeneity.

Figure 5 quantifies this mismatch: Asian flyways account for 33% of total studies and 30% of HPAI only studies, but only ~15% of domestic and ~8% of wild outbreak events. Conversely, Europe experienced ~46% of domestic and ~87% of wild outbreaks yet received only 23-25% of modeling attention, while the Americas experienced ~23% of domestic and ~5% of wild bird outbreaks compared to just 10% of modeling effort. Africa and the Middle East, which accounted for ~5% and ~11% of domestic outbreaks, have received no flyway-specific modeling attention.

This geographic concentration of modeling reflects historical epidemiological realities. HPAI H5N1 emerged and persisted in Southeast and East Asia from 1997 through 2020, driving intensive surveillance, data collection, and research investment in that region. During this period, Europe and the Americas experienced only sporadic, contained incursions that justified lower modeling priority. Additionally, the complexity of overlapping European migration routes across the Mediterranean, Atlantic, and trans-Saharan corridors made these flyways difficult to conceptualize as discrete modeling units, further discouraging mechanistic modeling investments when European outbreak risk appeared manageable.

However, this epidemiological landscape shifted dramatically after 2020. Europe and the Americas have experienced unprecedented outbreaks since 2021, with cumulative mortality and culling now exceeding historical Asian levels (Figures 6c,d and 7). Despite this documented shift in outbreak geography, modeling capacity remains concentrated in historically high-burden regions rather than current outbreak hotspots. This temporal lag in research focus, driven by historical rather than prospective epidemiological assessment, represents a critical gap in pandemic preparedness for the regions now driving global HPAI spread.

4.4. *Structural limitations of existing models*

Current mechanistic models for HPAI in migratory systems share several structural limitations. Most frameworks are limited to studying HPAI transmission within wild bird flocks, poultry, livestock, or within human only, without connecting them with each other through a transmission chain. We excluded such studies that were focused on secondary spillover only, such as poultry, without wild birds component [63, 64]. Analyzing the entire HPAI system would require a modeling framework in which the primary reservoirs, such as wild birds, are connected with the secondary and final spillover to humans. Additionally, compartmental frameworks dominate the literature (33.3%

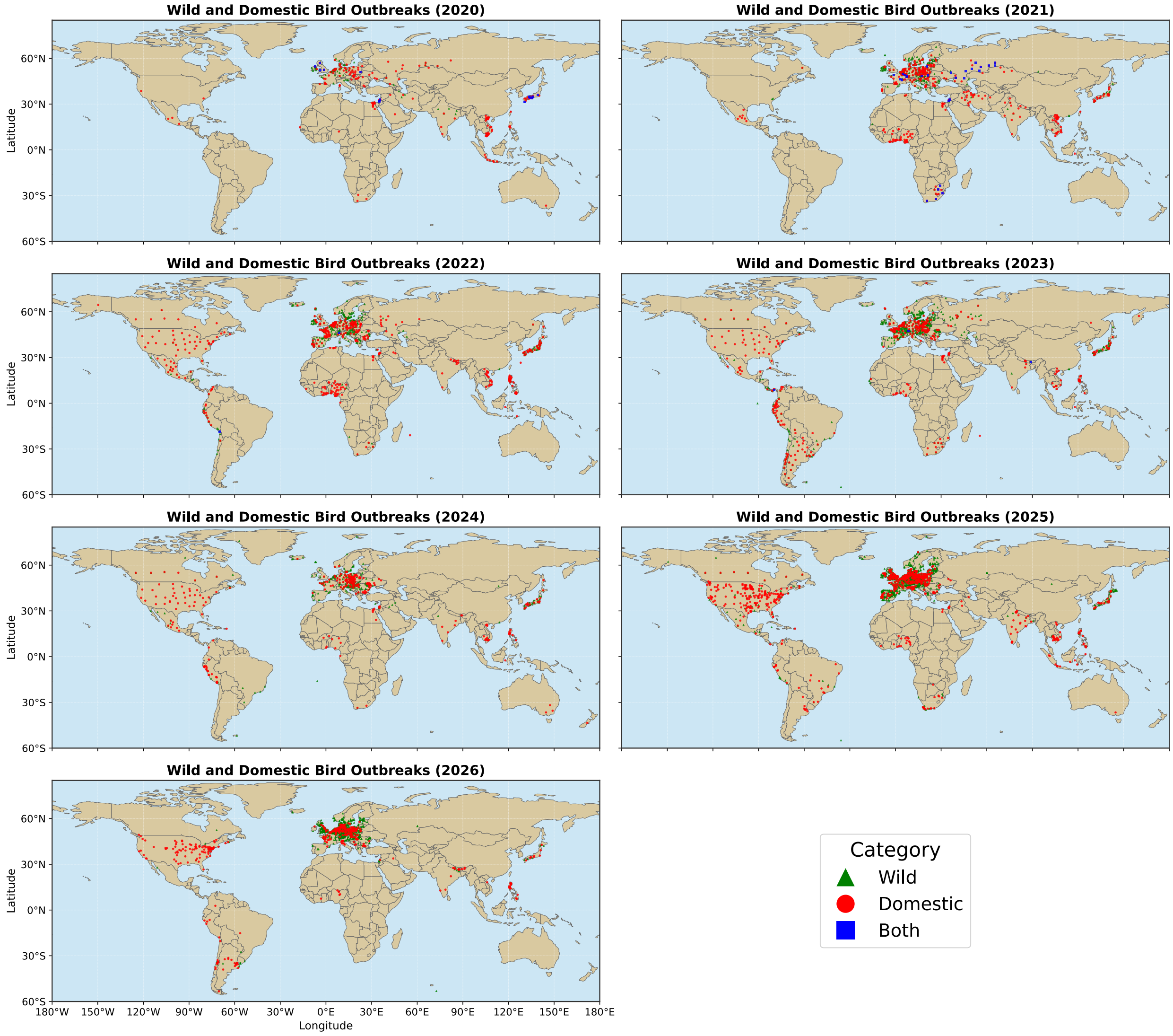


Figure 7: Spatial distribution of detected HPAI outbreaks by year (2020–2026) and host category (wild birds, domestic poultry, both), aggregated by region and reported to WOAH Health Information System (WAHIS) [53]. Data for 2026 is available until April (the time of writing this manuscript).

of studies) but typically assume homogeneous mixing within host populations, an assumption poorly suited to the heterogeneous contact structures characteristic of migratory systems. Mixed-species flocks at stopover sites exhibit pronounced variation in contact rates by species, age class, and behavioral guild, yet most models treat populations as well-mixed compartments. Similarly, species-specific differences in susceptibility, viral shedding, and migratory phenology are often collapsed into single "wild bird" compartments, obscuring the differential roles of reservoir versus spillover host species. The integration of empirical movement data from tracking studies into mechanistic frameworks also remains limited, with most models relying on simplified assumptions about migration routes and timing rather than incorporating observed individual movement trajectories.

4.5. Implications for pandemic preparedness and surveillance

The geographic and methodological gaps identified in this review have direct implications for HPAI surveillance and early warning. The concentration of modeling efforts in the East Asian-Australasian flyway reflects historical outbreak patterns but leaves other flyway systems, particularly those connecting Europe, Africa and America, without adequate predictive frameworks to guide surveillance resource allocation. Current models are predominantly retrospective, describing past outbreaks dynamics rather than providing prospective risk assessments tied to migration phenology. This limits their operational utility for early warning systems, which require spatially explicit, temporally resolved predictions of high-risk periods and locations. The absence of standardized modeling frameworks across flyway systems further complicates the development of coordinated international surveillance strategies, as risk assessments derived from different modeling approaches are difficult to compare or integrate across regions.

4.6. Future directions: toward integrated flyway-based models

Addressing the limitations identified in this review requires movement towards more integrated modeling approaches that explicitly link migration dynamics with transmission processes across spatial scales, ensuring that less studied wild bird flyways are considered. Future frameworks should incorporate empirical movement data from satellite tracking and bird ringing studies to replace simplified migration assumptions with biologically realistic movement parameters. An emerging opportunity lies in real-time tracking data and digital twin technologies: virtual replicas of migratory systems updated with live GPS tracking data (as demonstrated by [11] and [29]) could enable near-real-time predictions of high-risk transmission periods and dynamic scenario testing of surveillance strategies. Multi-species representations that account for differential susceptibility and contact heterogeneity among co-migrating species would substantially improve model realism. Equally important is the development of standardized parameterization protocols that enable cross-flyway comparisons and facilitate model transferability to data-poor regions. Integration of environmental drivers such as temperature, habitat availability, and land use into mechanistic frameworks would improve predictions of both migration timing and transmission risk; while a few studies (Section 3.5) demonstrated this feasibility, such integration remains underutilized in the HPAI modeling literature. Finally, improving data accessibility and transparency will be essential to foster interdisciplinary research and refine the predictive accuracy of public health outputs.

4.7. Limitations of this review

This review has several limitations that should be considered when interpreting its findings. The restriction to English-language publications may have excluded relevant modeling studies published in other languages, potentially contributing to the apparent geographic concentration of research in English-speaking regions. The heterogeneity of modeling approaches and inconsistent reporting of methodological details across studies complicated systematic comparisons of model structure and parameterization. Flyway classification of some studies required subjective judgment, particularly for studies with broad or ambiguous geographic scopes, which may introduce inconsistencies in the geographic distribution analysis. Additionally, this review organized models by wild bird migratory flyways ("vertical" north-south transmission corridors); mechanistic models emphasizing poultry industry trade networks ("horizontal" east-west transmission) as a primary focus were outside the scope, though these represent an important complementary transmission mechanism requiring separate systematic synthesis. Finally, the rapidly evolving nature of HPAI research means that relevant modeling studies may have been published or released during the review period, and ongoing. Consequently, updated review articles may be required in the future.

5. Conclusion

This systematic review reveals a pronounced geographic asymmetry in mechanistic HPAI modeling efforts: the East Asian–Australasian Flyway accounts for approximately one-third of all published work, while the American (10%) and European flyway systems, such as the Mediterranean–Black Sea and East Atlantic, together contribute approximately 25-30%, despite their ecological importance and sharply increasing HPAI burden since 2021. The East African-East Asian flyway was the most neglected flyway with no direct attention, while only two studies fall in that flyway (Table 3 and Fig. 3). Sensitivity analysis restricted to HPAI-specific models ($n = 20$) confirmed this pattern persists. This imbalance reflects detected historical outbreak geography and research funding patterns rather than current epidemiological risk, and it constitutes a substantive gap in global outbreak preparedness.

Across all flyways, compartmental ODE models are commonly deployed but frequently rely on homogeneous mixing assumptions and coarse spatial resolutions that obscure transmission dynamics at ecologically critical bottleneck sites such as wetlands and staging areas. Integration of empirical movement data from satellite telemetry and citizen science platforms remains limited, and cross-species heterogeneity in susceptibility and migration behavior is rarely captured.

Future mechanistic modeling efforts should prioritize understudied flyway systems, and adopt multi-species, multi-host frameworks that link wild bird migration dynamics to domestic poultry and human spillover risk along the full transmission chain. Standardized parameterization protocols, open data sharing, and integration of real-time tracking and outbreak surveillance data are essential for the development of spatially explicit, operationally useful early warning tools. Given the accelerating global spread of clade 2.3.4.4b H5N1, investment in these modeling capacities across all major flyways is now a One Health priority.

Declarations

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Declaration of Generative AI and AI-assisted Technologies: During the preparation of this work, the authors used Claude (Anthropic) to improve language clarity and readability. The authors reviewed and edited the final content and take full responsibility for its accuracy.

Data Availability Statement: All data supporting this systematic review will be made available upon request from the corresponding author. Search strategies and database exports are openly available via the Open Science Framework (`10.17605/OSF.IO/ECM2Z`). Outbreak data used in Figures 6 and 7 were obtained from WOAH WAHIS [53]. Flyway boundaries used in Figure 2 were obtained from BirdLife International [19].

Supporting Information:

Table S1: Search string structure and terms for HPAI mechanistic modeling systematic review.

Fig. S1: Geographical distribution of HPAI modeling studies by country of study focus.

Table 5: Characteristics of included studies (n=30) investigating HPAI transmission in migratory bird systems through mechanistic modeling.

Study	**Model type**	**HPAI subtype**	**Country/ Region**	**Flyway**	**Data type**	**Population type**
Llanos-Soto et al. 2025 [23]	Mathematical ODE model of SIR type	H5N1	Croatia	Mediterranean	Outbreak data	wild migratory birds + waterfowl species (migratory and non-migratory mallard, mute swan)
Takekawa et al. 2025 [24]	Agent-based model of SEIR type	H5N1	Mongolia	Central Asia + East-Asia Australasia	Empirical data from virological field samplings and markings of Swan Geese	Migratory flocks of Swan Geese
Yin et al. 2025 [11]	Individual/Agent-based model integrated with SIR model	H5N1 + H5N8	East Asian-Australasian region	East Asia-Australasia	GPS telemetry + eBird + Remote sensing + Poultry density	Wild birds and poultry
Castonguay et al. 2025 [25]	Spatial model (random forest, XGBoost and SEM)	General AIV (HPAI H5N1, also LPAI H9N2)	Bangladesh	East Asia-Australasia	Occurrence data, Reported AIV cases, Chicken census data, Climate projections, Land cover projections, Population density projections	Wild birds, poultry, humans, live bird markets
Mursel et al. 2025 [26]	Mathematical PDE of SIR type	H5N1	USA	Pacific + Central + Atlantic	eBird abundance data	Wild birds (mallard ducks)
Chanda et al. 2025 [27]	Mixed: Bayesian Network Modeling (BNM) + Stochastic PDE	H5N1 and H5N8	India (Kerala)	Central Asia	WOAH outbreak data (2014–2022) + Human census data (2011) + Questionnaire data (duck farmers) + Wetland classification	Domestic ducks (primary) + Migratory birds (source)
Ewing and Bouwhuis 2025 [28]	Individual-based model of SEIR type	H5N1	Germany	East Atlantic	Daily carcass counts	Wild birds
McDuie et al. 2024 [29]	Spatial model	H5N1	North America	Pacific + Central + Atlantic	GPS tracking data	Wild waterfowl
Schreuder et al. 2022 [30]	Spatial model	H5N1, H5N6 and H5N8	Netherlands	East Atlantic	wild bird count and poultry outbreaks	Wild birds and poultry
Yin et al. 2022 [31]	Mixed: Agent-based model + SIR (environmental transmission) + Migration network (site removal scenarios)	General AIV	Multiple along the flyway	East Asia-Australasia	GPS telemetry tracking, Global Lakes and Wetlands Database, ESA land cover, Birdlife International species distribution maps	Wild birds)
Pereira et al. 2020 [32]	Mathematical (fireworks) model	H5N1	Europe in general	Mediterranean + East Atlantic	OIE-WAHID notifications	Wild birds
Barnes et al. 2019 [33]	Stochastic branching process	H5/H7 (LPAI mutating to HPAI)	Australia	East Asia-Australasia	Literature and outbreak history	Poultry and wild birds as introduction source only
Rao 2019 [34]	Agent-Based Model of SEIR type	H5N1	Global	not specified	GIS data + BirdLife International Database + WHO outbreak maps	Wild birds
Lisovski et al. 2018 [35]	Mathematical ODE model of SIR type	General AIV	Netherlands	East Atlantic	Longitudinal surveillance data	Wild birds (mallard duck – partially migratory: residents + migrants)
Endo and Nishiura 2018 [36]	Mathematical ODE model of SIS type	General AIV	Flyway scale	East Asia-Australasia	Prevalence literature data – sample counts (positive/negative)	Wild birds (mallard, other ducks, swans/gulls/terns)
Zhang et al. 2017 [37]	Mathematical ODE model of SI-SEIR type	H7N9	China	East Asia-Australasia	Prevalence literature data – sample counts (positive/negative)	Wild birds + Domestic birds + Humans
Fourment et al. 2017 [12]	Mathematical Phylogeographic model - Continuous-time Markov chain	General AIV	USA and Canada	Pacific + Central + Atlantic	Genomic sequences	Wild birds (primary) + Poultry (sensitivity analysis)
Prosser et al. 2016 [38]	Spatial model	H5N1	China	Central Asia + East-Asia Australasia + East Asia - East Africa	Literature population estimates, H5N1 prevalence and remote sensing	Wild birds
Xu et al. 2016 [39]	Ecological Niche Model	H7N9	China	East Asia-Australasia	Human case data + Environmental data	Humans (primary outcome) + Poultry (as risk factors: live poultry farms, markets, processing factories) + Wild birds (migratory routes as risk factor)
Zhang 2016 [40]	Mathematical ODE model of SEIR type	H5N1	China	East Asia-Australasia	outbreak data + gene sequences + Population density + Bird migration flyway data	Domestic poultry + Humans + Wild birds
Brown et al. 2015 [41]	Stochastic SEIR network model	H5N1	Nigeria	Mediterranean + East Atlantic	Publicly available spatial data	Poultry, backyard ducks, wild birds, and humans
Zhang et al. 2014 [42]	Mathematical ODE model of SI-SEIR type	H7N9	China	East Asia-Australasia	Human case data	Wild birds (migratory + resident) + Domestic poultry + Humans
Rao 2014 [43]	Agent-Based Model of SEIR type	H5N1	Global	not specified	GIS data + BirdLife International+ GISAID EpiFlu sequences + GeoNames geocoding	Wild birds
Pandit et al. 2013 [44]	Mathematical ODE model of SIR-SIC type	H5N1	India	Central Asia + East Asia-Australasia	Outbreak data	Domestic poultry and wild birds
Tuncer & Martcheva 2013 [45]	Mathematical ODE (multiple types)	H5N1	Global (with focus on Indonesia, Egypt, Vietnam, China)	not specified	WHO cumulative human cases + FAO poultry outbreaks	Poultry (domestic birds) + Humans – wild birds as seasonal introduction source
Prosser et al. 2013 [46]	Spatial risk model	H5N1	China	Central Asia + East-Asia Australasia + East Africa - East Asia	Poultry distribution (1 km) + Waterfowl effective population (breeding/wintering) + Literature parameters (shedding, uptake, prevalence, biosecurity)	Domestic poultry (chickens, ducks, geese) + Wild birds (Anatidae waterfowl)
Alba et al. 2012 [47]	Agent/individual-based model	General AIV	Spain (Catalonia)	Mediterranean	Population censuses + AIV prevalence	Wild birds
Penny et al. 2010 [48]	Mathematical ODE model of SIR type	H5N1	Lake Constance (Europe)	East Atlantic + Mediterranean	Census data and dead H5N1 positive birds	Wild waterbirds
Henaux et al. 2010 [49]	Mathematical ODE model of SEIR type	General AIV (primarily H5N1 context, but also H5N2, H7N7)	Not country-specific	not specified	Laboratory challenge trials + field prevalence data	Wild birds (waterfowl – Anseriformes: ducks, geese, swans)
Bourouiba et al. 2010 [50]	Spatial dynamic model	H5N1	Mongolia (Breeding) → China (Stopovers & Breeding) → India (Wintering)	Central Asia	Satellite tracking data + Population estimates + Survival/reproductive parameters	Wild birds

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