



# Patterns of Avian Influenza Virus detection from active surveillance in wild birds: A systematic review and meta-analysis

Marie-Cécile Dupas<sup>a,b</sup>, Alessandra Falcucci<sup>c</sup>, Claudia Pittiglio<sup>c</sup>, Xavier Roche<sup>c</sup>,  
Giuseppina Cinardi<sup>c</sup>, Amy Delgado<sup>c</sup>, Ismaila Seck<sup>c</sup>, Madhur Dhingra<sup>c</sup>, Marius Gilbert<sup>a</sup>

<sup>a</sup> Université Libre de Bruxelles, Brussels, Belgium

<sup>b</sup> Hasselt University, Hasselt, Belgium

<sup>c</sup> The Food and Agriculture Organisation of the United Nations (FAO) Headquarters, Rome, Italy

## ARTICLE INFO

### Keywords:

Influenza A  
Meta-analysis  
Wild bird species  
Viral prevalence rate

## ABSTRACT

We summarised active surveillance data to identify patterns and ecological factors correlated with AIV detection in wild birds, through a systematic review and meta-analysis. We screened 2851 articles from the PubMed and Scopus databases, out of which 197 met our eligibility criteria and were selected for further analysis. The dataset encompassed 367 wild bird species from 72 avian families. The pooled prevalence of sampled birds was 4.80% (95% CI: [3.91–5.77%]) across 900,469 samples collected during the period 1971–2023, with substantial heterogeneity ( $I^2 = 99.7%$ ) across studies. Among continents, Central America displayed the highest prevalence at 9.89% (95% CI: [2.25–21.99%]), albeit based on relatively few samples ( $n=4205$ ). In temperate regions, prevalence peaked in autumn, at 5.82% (95% CI: [3.84–8.15%]), while in tropical regions, prevalence was notably higher during the dry season (2.33%, 95% CI: [0.38–5.54%]) than during the wet season (0.22%, 95% CI: [0.00–0.90%]). Prevalence varied significantly across avian families, with Anatidae, the most extensively sampled family, exhibiting a prevalence of 6.19% (95% CI: [5.10–7.37%]). Migratory species and those associated with freshwater habitats also exhibited higher AIV detection. Moreover, meta-regression analyses revealed that seasonal patterns of AIV detection differed across regions. Despite this, high heterogeneity across studies remained, likely driven by differences in surveillance intensity, diagnostic methods, and unmeasured ecological factors. This meta-analysis highlights key spatial, taxonomic, and temporal patterns in AIV prevalence among sampled birds. The findings underscore the need for harmonised, representative surveillance to better anticipate emerging avian influenza risks.

## 1. Introduction

Avian influenza (AI) is a viral disease of global importance, causing significant morbidity and mortality in wild and domestic birds and posing a risk of transmission to humans. It spreads directly via the faecal–oral route and indirectly through contaminated substrates such as food, water, or farm equipment. Long-distance transmission is primarily driven by wild migratory birds and further amplified by poultry trade and transport, which facilitate the virus's spread across regions and borders [1].

Wild birds, particularly waterfowl, are natural reservoirs for AIV and host a wide diversity of viral subtypes [2,3]. They typically carry low-pathogenicity avian influenza (LPAI) viruses without clinical signs, yet certain H5 and H7 LPAI lineages may mutate into highly pathogenic avian influenza (HPAI) after introduction into poultry populations.

While passive surveillance (dead or sick birds) maps where HPAI viruses emerge, many studies have instead focused on estimating AIV prevalence in specific wild bird species within defined regions and sampling periods to capture background circulation and silent reservoirs. Previous surveillance studies [4–8] have shown that the prevalence of AI in sampled wild birds varies geographically and can change over time. Collating these fragmented results into a comprehensive study is therefore highly insightful, but little effort has been made recently in this direction due to the considerable time required to compile and harmonise disparate data sets.

Early global reviews laid the groundwork for our understanding of AIV in wild birds. Olsen et al. (2006) [9] identified migration, aquatic lifestyle, and surface feeding as key ecological drivers of LPAI prevalence. Building on this, Munster and Fouchier (2009) [10] synthesised four decades of surveillance data to demonstrate the persistent,

\* Corresponding author at: Université Libre de Bruxelles, Brussels, Belgium.  
E-mail address: [mariececile.dupas@ulb.be](mailto:mariececile.dupas@ulb.be) (M.-C. Dupas).

seasonal circulation of LPAI in migratory waterfowl and highlighted major geographic and taxonomic gaps. Finally, Garamszegi and Moller (2007) [11] showed through comparative analysis that traits such as migration distance and freshwater habitat use significantly predict LPAI prevalence, underscoring the role of host ecology in shaping virus distribution.

Recently, meta-analyses have offered subtype-specific prevalence estimates (e.g., H5N6, H5N8, H9) and revealed substantial heterogeneity across host taxa, regions, and sampling methods [12–15]. In parallel, a few studies have examined overall AIV prevalence at the national or regional level, particularly in Asia, highlighting the variability between species and locations [8,16].

The objective of the present study is to synthesise prevalence data from sampled birds and investigate the ecological, taxonomic, and geographical drivers of AIV detection. This work aims to support the development of surveillance strategies to prevent the introduction and spread of the disease and reduce its impacts on both avian and human health.

## 2. Materials and methods

We conducted a systematic review of the literature concerning prevalence rates of sampled wild bird species. The complete database is presented in Table S1. The detailed list of bird species identified through the review is provided in Table S2.

### 2.1. Search strategy

The search strategy consisted in screening PubMed and Scopus, two English databases for scientific literature. The search strings used for the systematic review included “avian influenza”, “surveillance” or “incidence” or “prevalence”, “wild bird” or “waterfowl” or “migratory bird”, and combinations of these terms.

### 2.2. Study selection

All studies identified in searches were assessed for eligibility and inclusion by MCD. Systematic research and screening were started in September 2023, and the last systematic search was requested on September 20, 2024. Relevant research findings were then manually selected based on the relevance of the title and/or abstract to the prevalence of AIV in wild birds, as determined through active surveillance, PCR tests or virus isolation tests. Only studies containing primary data were considered in our review. The original authors of the selected publications were not contacted for additional information and unpublished data was not included.

### 2.3. Exclusion criteria

To refine the initial pool of studies identified through the search, we applied the following exclusion criteria to focus specifically on epidemiological studies addressing AIV in wild bird populations: (1) non-wild bird studies (domestic birds or mammals); (2) non-research-based publications such as press releases, newsletters, forum discussions, etc.; (3) studies missing information on location, sample size, prevalence, or detection rate; (4) studies based on fewer than 10 samples.

### 2.4. Data extraction

Data were extracted and placed in summary tables under the following headings (Table S1): reference, continent, country, location, scientific name of species, family of species, order of species, start and end year of study, months of sampling, sample size and number of positive cases. All species were reported in a separate table and a code identifier was assigned to identify each species reported in the database (Table S2).

## 2.5. Statistical analysis

Statistical analysis was performed using R Core Team (version 4.4.0) software [17] and the *meta* and *metafor* packages [18].

### 2.5.1. Statistical modelling framework

**Definitions.** In this study, we define the prevalence as the *prevalence of sampled birds* because it is the proportion of positive samples among the total number of birds sampled in each study, acknowledging that these estimates do not represent the true prevalence in the overall wild bird population.

Each prevalence value (i.e., each row in Table S1) was treated as a separate observation, defined as a unique combination of study, species, sampling month(s), year(s), and location (country). A single study can therefore contribute multiple observations when it reports results for multiple species, sampling periods, countries, or years (Fig. 1). For all analyses, we removed observations with fewer than 10 samples. The observations kept are marked as “Yes” in the column “Included\_in\_metaanalysis” of Table S1.

**Overall pooled prevalence.** To derive the overall pooled prevalence of sampled birds, we aggregated observations at the study level (Fig. 2). All eligible observations originating from the same study were combined by summing the total number of positive birds and the total number of birds sampled, resulting in one aggregated prevalence estimate per study.

**Subgroup analysis.** We performed subgroup analyses to explore how the prevalence of sampled birds varied across taxonomic, temporal, geographical, and ecological characteristics. Each subgroup analysis was conducted independently (Fig. 2).

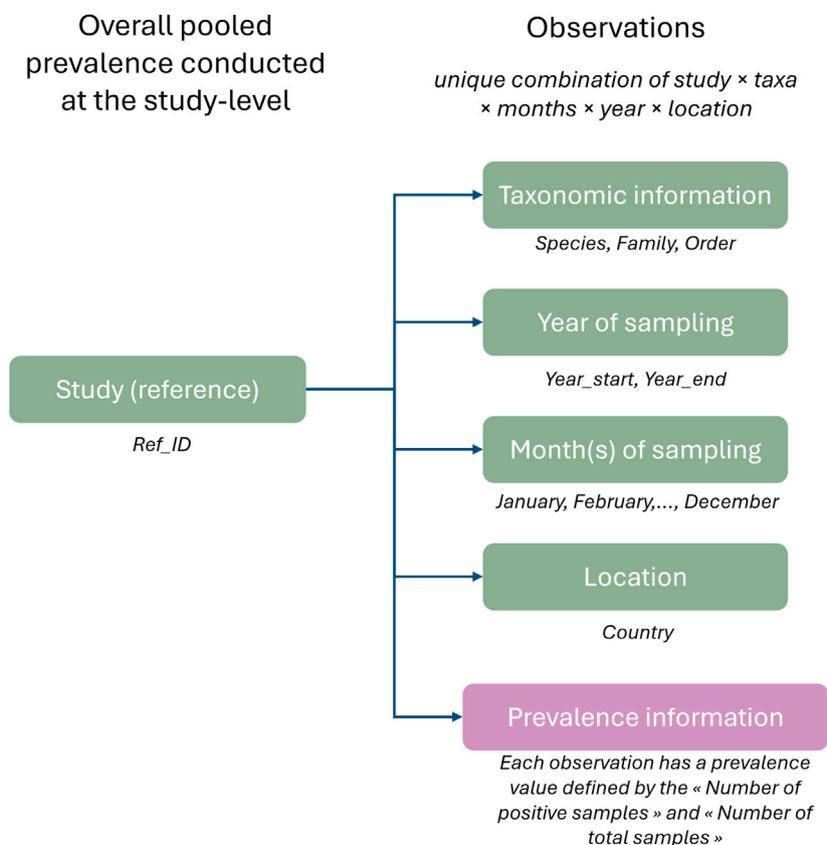
For taxonomic subgroup analyses, observations were aggregated at two levels: (i) the *study × species* level and (ii) the *study × family* level. This means that all observations within the same study that referred to the same species (or the same family) were combined by summing positives and total sampled birds, yielding one prevalence estimate per study–species or study–family combination. Taxonomic groupings were based on the scientific and family names reported in the original studies (Table S2). To ensure robust species-level estimates, we included only species with a cumulative sample size of at least 30 birds across all studies.

For the seasonal subgroup, observations were classified into four hemispheric categories based on the country of sampling (Northern, Southern, Tropical). Polar regions were excluded due to insufficient data. Observations spanning multiple countries from different hemispheres were also excluded from seasonal analyses. For the Northern and Southern Hemispheres, seasons were defined using a combination of “core” months (e.g. December–February for winter in the Northern Hemisphere) and adjacent “close” months (e.g. November and March). Observations spanning 1–4 months were assigned to the season that contained most of their core months, provided all sampled months fell within the core or close months of that season (Table S9); otherwise, no season was assigned.

For tropical regions, where temperate seasonal definitions do not apply, observations were instead classified as dry or wet season based on country-specific rainfall patterns. Season assignments were determined using published climatological data for each sampling location (see column “Tropic\_season” in Table S1). Observations spanning transition periods between dry and wet seasons, or exceeding four months, were excluded from seasonal analyses.

For continent-level subgroup analyses, observations were classified using standard continental categories (Africa, Asia, Europe, North America, South America, Central America, Oceania, Antarctica).

Ecological subgroup analyses were based on species-level traits extracted from the IUCN Red List [19], including habitat type (freshwater, marine, terrestrial) and migratory behaviour (full migrant, non-migrant, altitudinal migrant, nomadic).



**Fig. 1. Structure of the database used in the meta-analysis.** An observation is defined as a unique combination of study, taxonomic information (*species, family, order*), year(s) of sampling (“*Year\_start*”, “*Year\_end*”), month(s) of sampling (*January–December*), location (*country*), and prevalence information (*number of positive samples* and *total number of samples*).

**Definition of regions.** For temporal analyses (monthly prevalence subgroup analysis and meta-regression), broader geographic regions were defined based on hemispheric classification and data availability. Seasonal classification was first applied at the hemispheric level (Northern Hemisphere, Southern Hemisphere, Tropical, Polar). For monthly prevalence analyses and the “*Season × Region*” meta-regression, Northern Hemisphere observations were further stratified into three regions (Northern Hemisphere–Americas, Northern Hemisphere–Europe, Northern Hemisphere–Asia), as sufficient data were available to support this subdivision.

Accordingly, the term “region” in the manuscript refers specifically to these specific geographic groupings and is distinct from the continent categories used in subgroup analyses. These regional definitions apply only to monthly prevalence analyses and the “*Season × Region*” meta-regression model.

#### 2.5.2. Pooled prevalence estimates

After aggregating the data at the appropriate level (either at the study level for the overall pooled estimate or at the “*study × subgroup*” level for subgroup analyses), some resulting prevalence values were extremely low or extremely high (approaching 0 or 1), which leads to unstable sampling variances. To stabilise these variances, we applied the Freeman–Tukey double arcsine transformation. The transformed estimates were then pooled using inverse-variance weighting under a random-effects model. Final pooled prevalence values were back-transformed for interpretation.

#### 2.5.3. Publication bias

Publication bias occurs when study results are more likely to be published if they are positive or statistically significant. Therefore, we

assessed whether study size influenced reported prevalence values using both visual and statistical approaches. Publication bias was assessed only for the study-level pooled analysis and not within each subgroup.

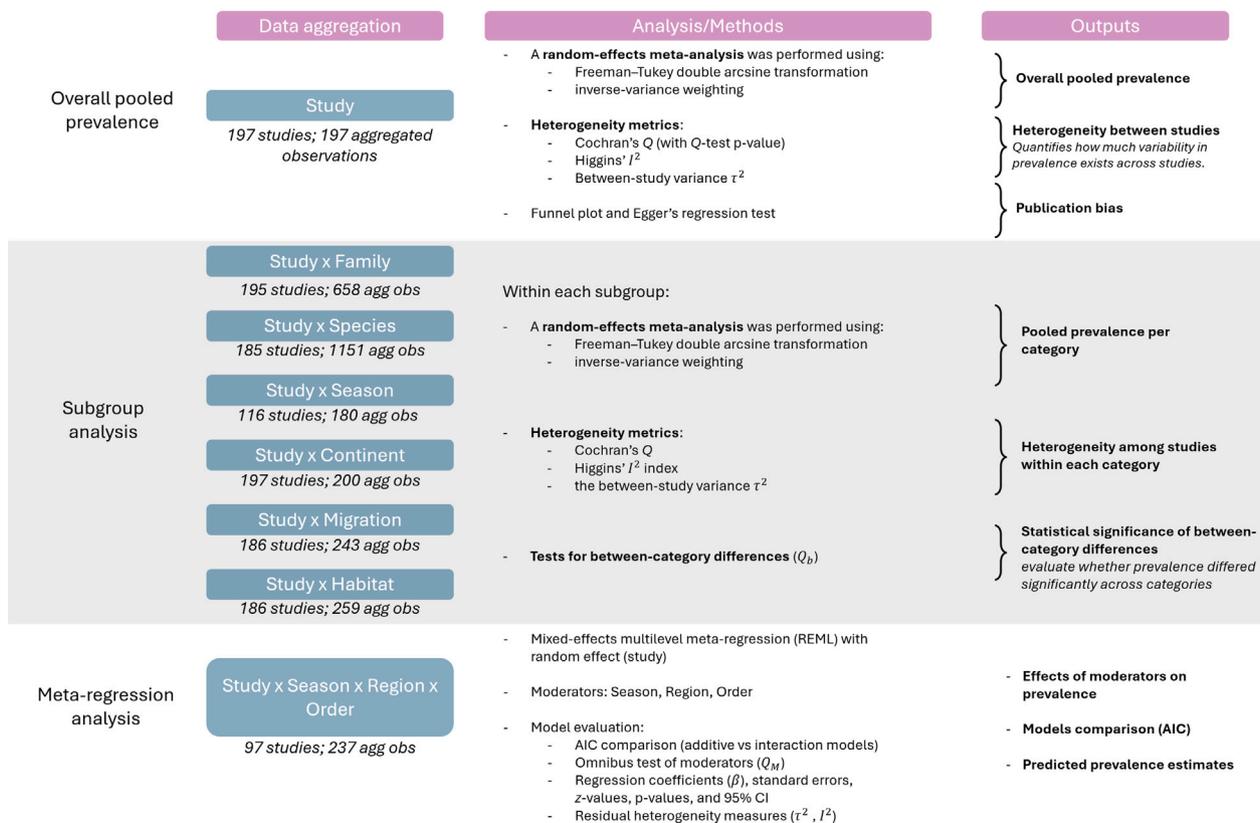
We first inspected funnel plot symmetry by plotting study-level prevalence estimates against their standard errors. Asymmetry in this plot may indicate that smaller studies tend to report systematically higher or lower prevalence values than larger studies, suggesting potential reporting bias.

We then applied Egger’s regression test [20], which formally evaluates whether study size is associated with deviations in estimated prevalence. A non-significant intercept indicates no statistically detectable asymmetry, whereas a significant result suggests the presence of small-study effects.

#### 2.5.4. Sampling bias

To evaluate whether sampling effort was systematically influenced by ecological characteristics of species, we conducted two complementary analyses. First, to assess whether more abundant species were sampled more intensively, we matched species-level sample counts with global population estimates obtained from the IUCN Red List [19]. We evaluated the correlations between total number of samples and estimated population size using Pearson and Spearman tests on log–log transformed values.

Second, to investigate whether sampling effort differed across migratory categories, each species was assigned a migratory behaviour (full migrant, non-migrant, altitudinal migrant, or nomadic) according to IUCN classifications. Total sample counts per species were compared across categories using a Kruskal–Wallis rank-sum test [21]. Pairwise differences were further evaluated with Dunn’s post-hoc tests and Benjamini–Hochberg correction [22], implemented in the DescTools R package [23].



**Fig. 2. Analysis workflow.** The diagram summarises the three analytical components of the study: the overall pooled prevalence, subgroup analyses, and the meta-regression. In the *Data aggregation* column, expressions such as “Study × Season” or “Study × Species” indicate the level at which observations were grouped before analysis. For example, all observations belonging to the same study and the same season were combined to produce a single prevalence estimate for that study–season category. For each aggregation level, the label below the box reports the number of studies ( $k$ ) and the number of aggregated observations used in that analysis. For subgroup analyses, categories refer to the distinct levels within each subgrouping variable (e.g., individual species, avian families, seasons, continents, migration behaviours, or habitat types).

These analyses were intended to identify potential biases in sampling intensity that might influence observed prevalence patterns. They were performed independently of the meta-analytic models and are reported in the Results section.

### 2.5.5. Heterogeneity measures

Heterogeneity measures the variability between studies beyond random chance, reflecting differences in study designs or populations. Heterogeneity between studies was assessed with three complementary metrics: (i) Cochran's  $Q$  for total heterogeneity (with  $Q$ -test  $p$ -value), (ii) Higgins'  $I^2$  index to express the proportion of total variation due to heterogeneity, and (iii) the between-study variance  $\tau^2$ . These measures were computed both for the overall pooled analysis and within each subgroup meta-analysis. High heterogeneity ( $I^2 > 75\%$ ) suggests substantial between-study differences, limiting the reliability of pooled estimates, whereas low heterogeneity ( $I^2 < 25\%$ ) indicates consistent results across studies. Quantifying heterogeneity using  $I^2$  and  $\tau^2$  is thus essential both to interpret pooled estimates and to identify sources of variability [24].

For subgroup analyses, we also assessed differences between subgroups using the between-group  $Q$ -test (denoted  $Q_b$ ). A significant  $Q_b$  ( $p < 0.05$ ) indicates that prevalence differs more across subgroups than would be expected by chance alone.

### 2.5.6. Meta-regression analysis

The meta-regression analysis complements the subgroup analyses by evaluating multiple variables simultaneously. Prior to meta-regression,

observations were aggregated at the “study × season × region × taxonomic order” level by summing positive and total samples, yielding one prevalence estimate per study–moderator combination (Fig. 2). We fitted multilevel mixed-effects meta-regression models using restricted maximum likelihood (REML) via the `rma.mv` function in the `metafor` package [18] to evaluate moderators of AIV prevalence. A random intercept for study was included to account for non-independence of multiple observations from the same study.

We considered three categorical moderators: season (Winter [reference], Spring, Summer, Autumn), region (Northern Europe [reference], Northern Americas, Northern Asia, Southern Hemisphere), and taxonomic order (Anseriformes [reference], Charadriiformes, Gruiformes, Passeriformes, Pelecaniformes, Suliformes). We first fitted single-moderator models to assess individual effects, then compared additive and interaction models for several moderator combinations using Akaike Information Criterion (AIC). Based on model comparison, we retained two final models: (1) a seasonal model with the Season × Region interaction, and (2) a taxonomic model with Order alone.

We report the omnibus test of moderators ( $Q_M$ ), regression coefficients ( $\beta$ ) on the Freeman–Tukey scale with standard errors, z-values, p-values, and 95% confidence intervals. Predicted prevalences were back-transformed for interpretation.

## 3. Results

### 3.1. Data description: locations, years, seasons, and species

A total of 2851 studies were identified from two international databases (Scopus and PubMed). After reviewing the titles, abstracts,

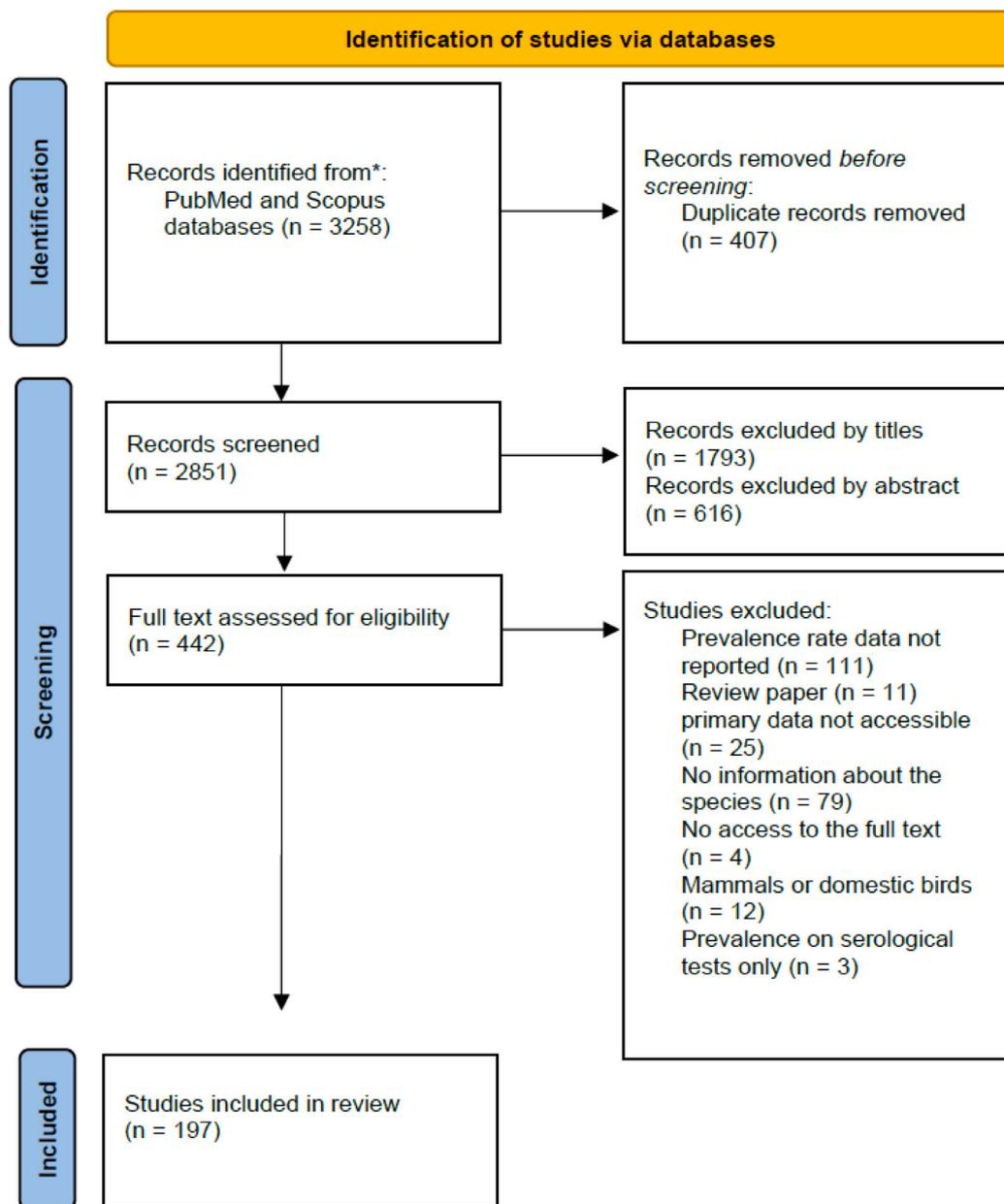


Fig. 3. Flow Diagram PRISMA [25].

and full texts, 197 articles were accepted (Fig. 3). The full list of references is presented in Table S3. These articles provided 4325 observations classified by reference, taxonomic information, months of sampling, year of sampling, and location (Table S1). A single study may provide multiple observations depending on the level of detail of the information reported. All raw data are provided in Table S1. We removed observations with fewer than 10 samples in the meta-analysis, resulting in a final dataset comprising 900,469 samples tested for AIW in wild birds for 2512 observations from 197 studies.

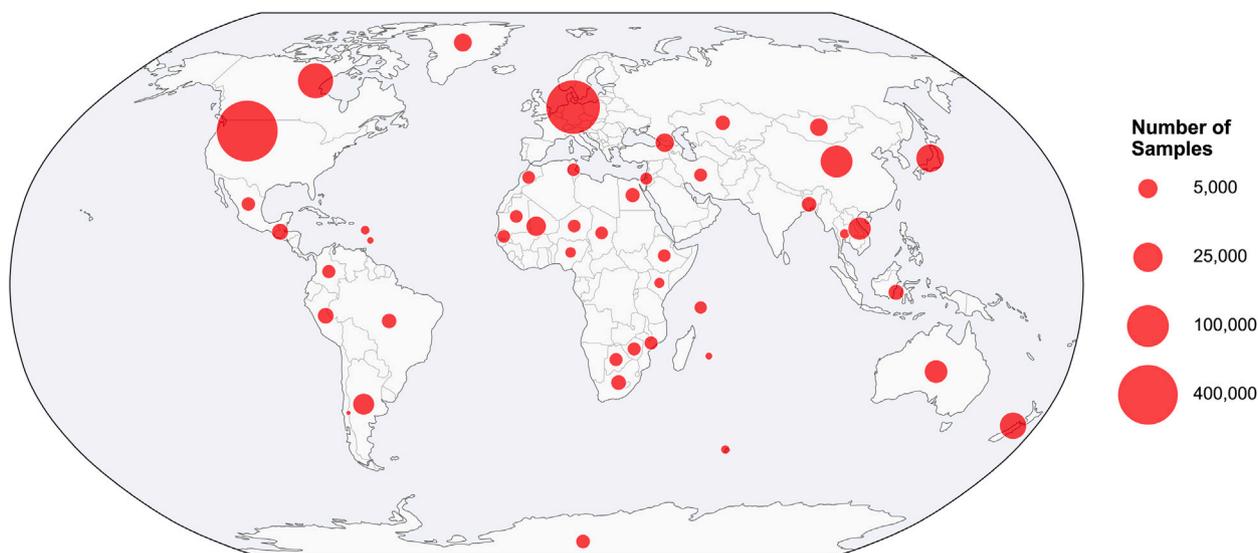
Data were collected between 1971 and 2023. Most samples were collected in North America (54% of total samples), followed by Europe (29% of total samples), and Asia (8.9%). Countries with the most sampling effort were: United States (434,865 samples), The Netherlands (144,035 samples), Canada (50,898 samples), China (34,894 samples) and Russia (20,988 samples) (Figs. 4(a) & 4(b)).

Prevalence rate estimates of sampled birds were predominantly reported at the species level, accounting for 825,237 samples. In contrast,

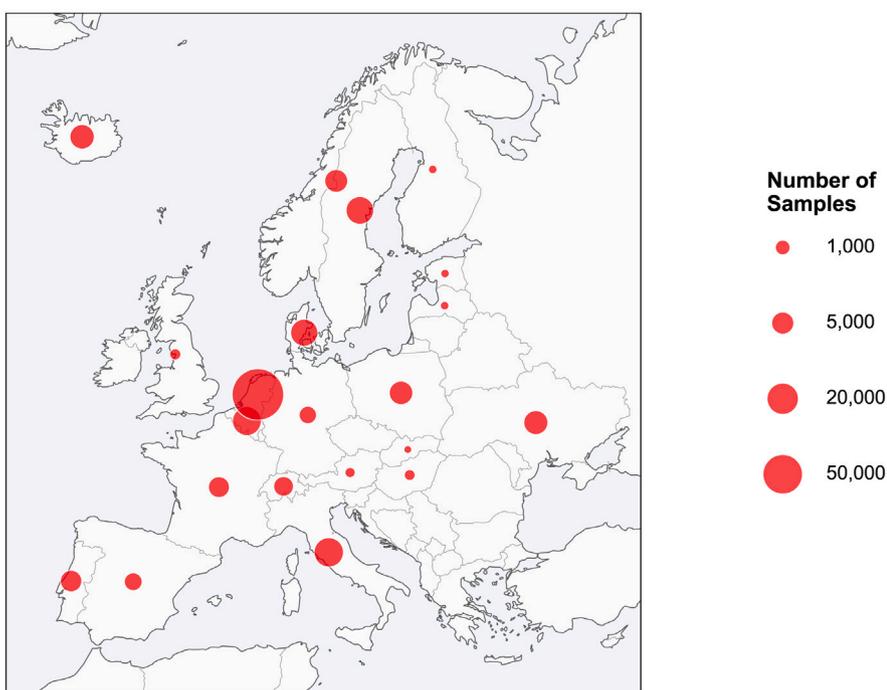
only a small proportion of the studies provided data at the family level (6.6%, 59,037 samples), the order level (1.4%, 12,405 samples) or the genus level (0.4%, 3790 samples). Most of the samples were collected from species within the order Anseriformes (81%), followed by Charadriiformes (13%) and Passeriformes (2%) (Table S5).

We investigated whether the sampling effort was influenced by the global abundances of species. Among species with a valid scientific name, 234 had both sample counts and population size estimates available from the IUCN Red List. On the log–log scale, neither Pearson ( $r = -0.10$ ,  $p = 0.12$ ) nor Spearman ( $\rho = -0.096$ ,  $p = 0.14$ ) correlations were statistically significant, indicating that common and rare species were sampled with comparable intensity.

We next examined whether sampling effort differed by migratory behaviour (Section 2.5.4). Species were classified as altitudinal migrants, full migrants, nomadic, or non-migrants (IUCN classification), and total sample counts per species were compared. A Kruskal–Wallis



(a) World map



(b) Focus on Europe

**Fig. 4.** Number of samples per country reported in the database of the literature review.

test showed no significant overall difference in sampling effort across migration categories ( $\chi^2 = 6.84$ ,  $df = 3$ ,  $p = 0.08$ ). Full migrants tended to have the highest median sample counts and non-migrants the lowest. Post-hoc pairwise Dunn tests with Benjamini–Hochberg correction revealed no significant differences between any two groups (all adjusted  $p > 0.33$ ). Together, these results indicate that neither the overall abundance of species nor their migratory behaviour systematically biased the number of samples collected. A complementary analysis comparing sampling effort between dabbling and diving ducks showed no evidence of differential sampling intensity between these ecological groups (Figure S3).

### 3.2. Overall pooled prevalence

We first evaluated the overall pooled prevalence of sampled birds by aggregating data at the study level, regardless of species, seasons, or other stratifications, resulting in one aggregated data point per study. A total of 197 studies were included, accounting for 900,469 samples, of which 63,731 were positive for AIV, for a pooled meta-analysis prevalence of 4.80% (95% CI [3.91–5.77%]). The forest plot displaying the study-specific prevalence estimates is presented in Figure S1.

Substantial heterogeneity was observed ( $I^2 = 99.7\%$ ;  $\tau^2 = 0.0226$  [0.0198;0.0308]), indicating significant variability between studies. The funnel plot (Figure S2) showed slight asymmetry, but Egger’s test

did not provide statistically significant evidence of publication bias ( $p = 0.3610$ ). The heterogeneity likely arises from differences in study designs, regions, and taxonomic levels, underscoring the importance of subgroup analyses.

### 3.3. Exploration of heterogeneity and subgroup analysis

Given the diversity of the studies included in the meta-analysis, an exploration of heterogeneity was carried out to assess the variability in prevalence rates of sampled birds. Subgroup analyses were performed by taxonomic levels, seasons, and continents to better understand the sources of this variability.

#### 3.3.1. Taxonomic subgroup analysis

**Species-level analysis.** To evaluate heterogeneity at the species level, we conducted a subgroup meta-analysis including all species with a total sample size of 30 or more. A total of 367 species were included in the analysis, with results presented in Figure S4 and Table S7.

The test for subgroup differences confirmed significant variation in prevalence across species ( $Q_b = 2,520$ ,  $p < 0.0001$ ), indicating strong taxonomic influences on AI prevalence. High heterogeneity ( $I^2 > 75\%$ ) was observed across multiple species, particularly those with larger datasets. Heterogeneity tended to increase with the number of studies reporting a given species. For instance, *Anas platyrhynchos* ( $I^2 = 99.7\%$ ,  $\tau^2 = 0.0286$ ) was reported in 92 studies, highlighting substantial variability in prevalence estimates (Pooled prevalence = 9.27%, 95% CI: [7.29%–11.45%]). Similarly, *Anas crecca* (Pooled Prevalence = 7.71%, 95% CI: [5.51%–10.23%],  $I^2 = 95.6\%$ ) and *Anas carolinensis* (5.81%, 95% CI: [3.43–8.74%],  $I^2 = 99.5\%$ ) exhibited high levels of heterogeneity.

Pooled prevalence of sampled birds varied widely across species. *Anas poecilorhyncha* exhibited the highest prevalence at 44.6% (95% CI: [39.4–49.9%]), based on 368 samples collected across two studies; heterogeneity was low ( $I^2 = 5.5\%$ ,  $\tau^2 < 0.0001$ ,  $p = 0.3035$ ), indicating consistent estimates between those investigations. *Aix galericulata* showed a prevalence of 36.96% (95% CI: [23.49–51.49%]) from a single study of only 46 samples, reflected by its wide confidence interval. *Cairina moschata* had a pooled prevalence of 18.24% (95% CI: [14.67–22.10%]) based on 421 samples from three studies, with no detectable heterogeneity ( $I^2 = 0\%$ ,  $\tau^2 = 0$ ,  $p = 0.9685$ ). Although these species exhibited notably high prevalence rates, their sample sizes were relatively small, and estimates should be interpreted with caution.

**Family-level analysis.** As with the species-level analysis, only observations with available family or species information were included. This analysis, covering 72 avian families, estimated pooled prevalence and assessed heterogeneity using a random-effects model, while accounting for variability between families (Figure S5 and Table S8).

The test for subgroup differences confirmed statistically significant variation in prevalence among families ( $Q_b = 361.74$ ,  $p < 0.0001$ ). Anatidae was the most well-sampled family, with 162 studies covering 723,962 samples, yielding a pooled prevalence of 6.19% (95% CI: [5.10–7.37%]) and high heterogeneity ( $I^2 = 99.7\%$ ). The substantial heterogeneity suggests strong ecological and geographical influences on AI prevalence within this family. Laridae (70 studies, 73,785 samples) and Scolopacidae (49 studies, 31,621 samples) exhibited lower prevalence estimates (1.71%, 95% CI: [0.97–2.61%] and 1.35%, 95% CI: [0.49–2.52%]) but still displayed high heterogeneity ( $I^2 > 96\%$ ), indicating variability among studies within these families. Among other relatively well-sampled families, Phoenicopteridae (6 studies, 648 samples) had a prevalence of 3.86% (95% CI: [0.00–13.9%]), while Jacanidae (3 studies, 563 samples) had 2.19% prevalence with no observed heterogeneity ( $I^2 = 0\%$ ). Families such as Parulidae (5.94%) and Cardinalidae (13.7%) also exhibited relatively high pooled prevalence.

#### 3.3.2. Continent-level subgroup analysis

A subgroup analysis was conducted to examine AI prevalence across different continents (Table 1). The test for subgroup differences was statistically significant ( $Q_b = 140.67$ ,  $p < 0.0001$ ), indicating that prevalence estimates differed meaningfully across continents. The high heterogeneity in most regions ( $I^2 > 95\%$ ) suggests that additional ecological, taxonomic, and methodological factors may influence observed prevalence rates. Only Antarctica exhibited no heterogeneity ( $I^2 = 0\%$ ), likely due to the limited number of studies ( $k=2$ ) and near-zero prevalence.

The pooled prevalence estimates varied substantially, ranging from 0.0001% (95% CI: [0.0000–0.0032%]) in Antarctica to 9.89% (95% CI: [2.25–21.99%]) in Central America (Table 1). North America (6.11%, 95% CI: [4.61–7.80%]) and Europe (5.44%, 95% CI: [3.70–7.48%]) exhibited the highest prevalence rates among well-sampled regions, while South America had a notably low prevalence (0.09%, 95% CI: [0.00–0.47%]). Oceania exhibited a moderate pooled prevalence (4.29%, 95% CI: [0.51–11.35%]). The forest plot (Figure S8) completes this analysis providing a visual representation of prevalence estimates for each study across continents.

These results suggest potential regional differences in surveillance efforts, host species distribution, and environmental conditions affecting AIV circulation.

#### 3.3.3. Season-level subgroup analysis

Seasonal variation in AIV prevalence was evaluated using the season classifications derived from the month-based decision rules described in the Methods (Section 2.5.1). For temperate regions (Northern and Southern Hemispheres), observations were assigned to winter, spring, summer, or autumn; for tropical regions, observations were classified as dry or wet season based on country-specific rainfall patterns. Studies with sampling periods exceeding four months, or spanning transition periods, were excluded from this analysis. After filtering, 180 study-season strata remained, representing 256,763 sampled birds and 21,143 positive detections.

Pooled prevalence estimates, heterogeneity statistics, and sample sizes for each season are reported in Table 1. Overall, the random-effects model estimated a pooled prevalence of 3.90% (95% CI: [2.99–4.91%]) across all seasons combined, with substantial residual heterogeneity ( $I^2 = 99.3\%$ ,  $\tau^2 = 0.0248$ ).

In temperate regions, seasonal patterns showed notable variation. Autumn exhibited the highest prevalence at 5.82% (95% CI: [3.84–8.15%]), followed by summer at 5.36% (95% CI: [3.02–8.28%]). Winter displayed a moderate prevalence of 3.46% (95% CI: [2.17–5.02%]), while spring had the lowest estimate at 1.88% (95% CI: [0.57–3.78%]). Across all seasons, heterogeneity remained very high ( $I^2 > 95\%$ ), indicating that studies within a given season still varied widely in their reported prevalence.

In tropical regions, a marked difference was observed between dry and wet seasons. Dry season prevalence was 2.33% (95% CI: [0.38–5.54%];  $k = 10$ ), approximately ten-fold higher than wet season prevalence at 0.22% (95% CI: [0.00–0.90%];  $k = 8$ ).

The test for subgroup differences was statistically significant ( $Q_b = 46.24$ ,  $p < 0.0001$ ), indicating that prevalence differed substantially across seasonal categories. However, the consistently high within-season heterogeneity suggests that seasonal effects are only one of multiple factors shaping the variability observed among studies.

Monthly prevalence estimates were further explored by region using observations with a maximum sampling duration of three months (Figure S7). These analyses provide additional temporal resolution and broadly support the seasonal patterns identified in the subgroup analysis. In the Northern Hemisphere, prevalence tended to peak during summer and autumn in Europe, during autumn and March in Asia, and in early autumn (September–October) in North America. Tropical regions have slightly higher estimates in January–March, and Southern Hemisphere prevalence displayed two peaks in February and July. However, data from the Southern Hemisphere and tropical regions were comparatively sparse, limiting the robustness of monthly estimates for these regions.

**Table 1**

Pooled prevalence estimates of avian influenza virus (AIV) detection in wild birds by season (temperate and tropical), geographical region and avian families with more than 2000 samples. The table reports the number of studies ( $k$ ), pooled prevalence of sampled birds (%), 95% confidence intervals (CI), heterogeneity metrics ( $\tau^2$ ,  $\tau$ ,  $Q$ ,  $I^2$ ), and the number of samples and positive cases for each category.

| Subgroup           | $k$ | Prev. (%) | 95%-CI (%)   | $\tau^2$ | $\tau$ | $Q$       | $I^2$ | No. samples | No. positives |
|--------------------|-----|-----------|--------------|----------|--------|-----------|-------|-------------|---------------|
| Season (Temperate) |     |           |              |          |        |           |       |             |               |
| Winter             | 41  | 3.46      | [2.17–5.02]  | 0.0136   | 0.1165 | 2747.63   | 98.5% | 88 572      | 4610          |
| Spring             | 27  | 1.88      | [0.57–3.78]  | 0.0190   | 0.1379 | 544.08    | 95.2% | 28 330      | 577           |
| Summer             | 49  | 5.36      | [3.02–8.28]  | 0.0397   | 0.1992 | 16 341.03 | 99.7% | 74 452      | 10 244        |
| Autumn             | 45  | 5.82      | [3.84–8.15]  | 0.0209   | 0.1447 | 2151.23   | 98.0% | 53 775      | 5258          |
| Season (Tropical)  |     |           |              |          |        |           |       |             |               |
| Dry                | 10  | 2.33      | [0.38–5.54]  | 0.0153   | 0.1235 | 593.90    | 98.5% | 8497        | 439           |
| Wet                | 8   | 0.22      | [0.00–0.90]  | 0.0027   | 0.0517 | 32.04     | 78.2% | 3137        | 15            |
| Continent          |     |           |              |          |        |           |       |             |               |
| Africa             | 20  | 3.25      | [1.39–5.71]  | 0.0144   | 0.1198 | 266.93    | 92.9% | 24 316      | 668           |
| Antarctica         | 2   | 0.01      | [0.00–0.32]  | 0        | 0      | 0.04      | 0.0%  | 870         | 1             |
| Asia               | 35  | 4.07      | [2.13–6.56]  | 0.0261   | 0.1617 | 3426.34   | 99.0% | 105 554     | 2720          |
| Central America    | 6   | 9.89      | [2.25–21.99] | 0.0431   | 0.2075 | 337.50    | 98.5% | 4205        | 519           |
| Europe             | 50  | 5.44      | [3.70–7.48]  | 0.0213   | 0.1459 | 7167.57   | 99.3% | 248 975     | 15 663        |
| North America      | 66  | 6.11      | [4.61–7.80]  | 0.0182   | 0.1349 | 35 251.78 | 99.8% | 476 871     | 37 663        |
| Oceania            | 9   | 4.29      | [0.51–11.35] | 0.0419   | 0.2046 | 9268.17   | 99.9% | 26 464      | 6457          |
| South America      | 12  | 0.16      | [0.00–0.56]  | 0.0017   | 0.0411 | 52.85     | 79.2% | 13 214      | 40            |
| Family             |     |           |              |          |        |           |       |             |               |
| Anatidae           | 162 | 6.19      | [5.10–7.37]  | 0.0214   | 0.1463 | 59 313.10 | 99.7% | 723 962     | 59 383        |
| Laridae            | 70  | 1.71      | [0.97–2.61]  | 0.0119   | 0.1089 | 2391.55   | 97.1% | 73 785      | 2211          |
| Scolopacidae       | 49  | 1.35      | [0.49–2.52]  | 0.0161   | 0.1268 | 1492.92   | 96.8% | 31 621      | 902           |
| Rallidae           | 39  | 0.47      | [0.17–0.87]  | 0.0014   | 0.0379 | 88.40     | 57.0% | 8060        | 99            |
| Charadriidae       | 25  | 0.00      | [0.00–0.25]  | 0.0029   | 0.0535 | 73.87     | 67.5% | 4883        | 30            |
| Phalacrocoracidae  | 24  | 0.54      | [0.00–1.71]  | 0.0081   | 0.0900 | 124.56    | 81.5% | 2932        | 60            |
| Phasianidae        | 12  | 0.00      | [0.00–0.06]  | 0.0006   | 0.0235 | 13.24     | 16.9% | 2751        | 7             |
| Ardeidae           | 17  | 0.02      | [0.00–0.35]  | 0.0014   | 0.0377 | 28.35     | 43.6% | 2573        | 15            |
| Spheniscidae       | 6   | 0.19      | [0.00–0.97]  | 0.0029   | 0.0538 | 25.88     | 80.7% | 2322        | 12            |
| Passeridae         | 11  | 0.78      | [0.00–3.47]  | 0.0098   | 0.0989 | 26.34     | 62.0% | 2067        | 27            |
| Parulidae          | 5   | 5.94      | [0.00–37.34] | 0.2015   | 0.4489 | 132.48    | 97.0% | 2018        | 28            |

### 3.4. Meta-regression analysis

We first evaluated the effect of each moderator separately using single-moderator multilevel meta-regression models with a random intercept for study ( $k = 237$  observations from 97 studies). Taxonomic order showed the strongest effect ( $Q_M = 1944.8$ ,  $p < 0.001$ ), followed by season ( $Q_M = 1406.0$ ,  $p < 0.001$ ). Region alone was not significant ( $Q_M = 3.21$ ,  $p = 0.360$ ).

We then tested whether seasonal patterns varied across regions by comparing additive and interaction models. The model including the Season  $\times$  Region interaction showed substantially better fit than the additive model ( $\Delta AIC = 892$ ), indicating that seasonal dynamics of AIV prevalence differ significantly across regions (Fig. 5A, Table S10). In Northern Europe, prevalence peaked in autumn (3.3%, 95% CI: [2.5–4.3%]) and was lowest in spring (0.7%, 95% CI: [0.3–1.1%]). In contrast, Northern Americas showed a summer peak (2.2%, 95% CI: [1.6–2.8%]) with lower autumn prevalence (1.1%, 95% CI: [0.7–1.5%]). Northern Asia displayed a more stable pattern across seasons, with the highest prevalence in spring (1.7%, 95% CI: [0.9–2.6%]).

Regarding taxonomic reservoirs, Anseriformes (waterfowl) exhibited the highest predicted prevalence (2.0%, 95% CI: [1.5–2.5%]), followed by Suliformes (1.7%, 95% CI: [1.0–2.5%]), which did not differ significantly from Anseriformes ( $p = 0.31$ ). All other orders showed significantly lower prevalence compared to Anseriformes: Charadriiformes (0.5%, 95% CI: [0.4–0.6%]), Passeriformes (0.4%, 95% CI: [0.2–0.7%]), Pelecaniformes (0.4%, 95% CI: [0.2–0.6%]), and Gruiformes (0.3%, 95% CI: [0.2–0.5%]) (all  $p < 0.001$ ; Fig. 5B, Table S10).

We also explored whether major outbreak periods influenced prevalence by adding sampling period (pre-2005, 2005–2014, 2015–2019, post-2020) as an additional moderator. These periods were chosen to reflect known events in AIV epidemiology, including the initial spread of H5N1 (2005–2006) [26], the emergence of H5N8 (2014–2015) [27], and the dominance of clade 2.3.4.4b after 2020 [28]. However, no period differed significantly from the pre-2005 baseline (all  $p > 0.17$ ),

and the omnibus test of moderators was not significant ( $Q_M = 2.50$ ,  $p = 0.475$ ). Adding Period to the Season  $\times$  Region model did not improve fit ( $\Delta AIC = -7.8$ ). Because temporal period had no detectable effect on prevalence, this variable was not retained in the final meta-regression. Note that only 13 observations were available for the post-2020 period, limiting statistical power to detect recent changes in prevalence.

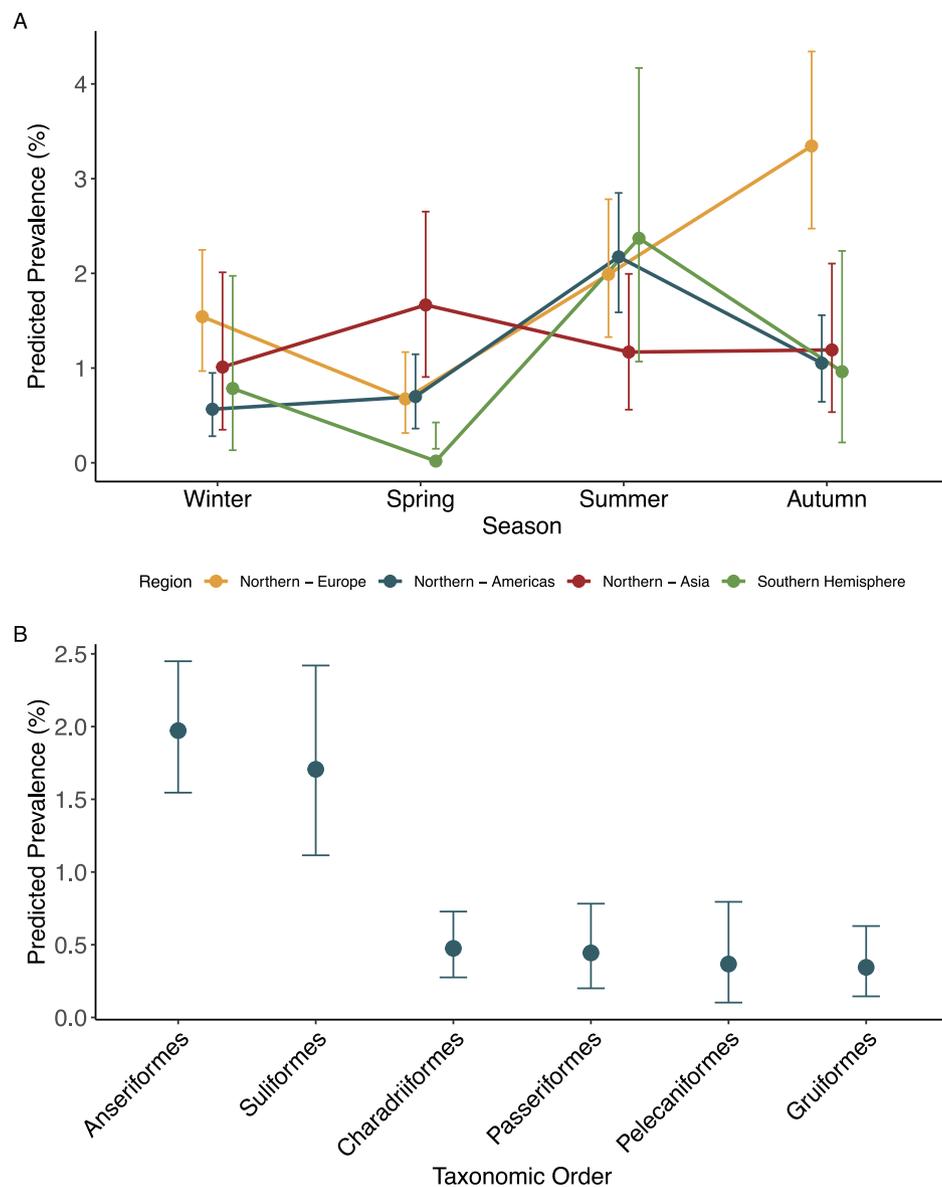
### 3.5. Exploration of ecological factors

As species-level subgroup analysis revealed strong taxonomic influences on AIV prevalence (Section 3.3.1), we next examined two ecological traits that might further explain variation in prevalence: habitat and migration behaviour. These characteristics were not reported in the original studies; therefore, we annotated each species post hoc from external IUCN data sources: primary habitat (freshwater, marine, or terrestrial) and migration behaviour (altitudinal migrant, full migrant, nomadic, or non-migrant). As these annotations are based on general IUCN species-level data, they may not capture local habitat or migratory variability at specific sampling sites. After excluding any entries lacking information from the IUCN database, 234 species remained.

**Meta-analysis by migration behaviour.** We performed a random-effects meta-analysis stratified by migration behaviour. The overall pooled prevalence was 3.92% (95% CI [3.15%–4.77%]), with high heterogeneity ( $\tau^2 = 0.0230$  [0.0197–0.0293],  $I^2 = 99.6%$ ). Stratified results are detailed in Table 2.

A between-group Q-test confirmed significant differences across migration categories ( $Q_b = 41.26$ ,  $df = 3$ ,  $p < 0.0001$ ). Full migrants exhibited the highest pooled prevalence (~5%), whereas resident species showed much lower prevalence (~0.8%). Altitudinal migrants carried effectively no detectable AIV, and nomadic species had a high prevalence rate, but there were fewer studies on nomadic species.

**Meta-analysis by habitat.** The overall pooled prevalence when stratifying by primary habitat was 3.65% (95% CI [2.92%–4.45%]),



**Fig. 5. Meta-regression predicted AIV prevalence in wild birds.** Error bars indicate 95% CI; predictions back-transformed from Freeman–Tukey scale. **(A) Seasonal model:** predicted prevalence across seasons by region (“Season × Region” interaction). **(B) Taxonomic model:** predicted prevalence by avian order.

with extremely high between-study heterogeneity ( $\tau^2 = 0.0232$  [0.0198–0.0290],  $I^2 = 99.6\%$ ,  $Q = 66$  013.45,  $df = 258$ ,  $p < 0.0001$ ).

A between-group Q-test confirmed that these three habitat categories differed significantly in pooled prevalence ( $Q_b = 63.41$ ,  $df = 2$ ,  $p < 0.0001$ ). The meta-analysis stratified by habitat revealed that freshwater-associated species exhibit the highest pooled prevalence of AIV (Table 2), with high heterogeneity ( $I^2 = 99.7\%$ ). In contrast, marine species (42 studies) had a substantially lower pooled prevalence of 0.47% (95% CI 0.10%–1.04%), with lower heterogeneity ( $I^2 = 86.2\%$ ). Terrestrial birds (39 studies) showed an almost equally low pooled prevalence of 0.45% (95% CI 0.00%–1.64%), but the wide confidence interval and high heterogeneity ( $I^2 = 88.8\%$ ) reflect both small sample sizes and inconsistent findings.

In summary, freshwater-associated birds carry AIV at substantially higher average rates than either marine or terrestrial birds, although all three groups exhibit considerable within-category heterogeneity.

#### 4. Discussion

This study provides the most extensive systematic review and meta-analysis to date of active surveillance data on avian influenza virus

(AIV) in wild birds. Although the pooled prevalence was 4.80% (95% CI: [3.91–5.77%]), this value reflects the proportion of positives among sampled individuals, not the true prevalence in wild populations, as surveillance efforts rely on opportunistic rather than population-based sampling. The substantial heterogeneity observed ( $I^2 > 99\%$ ) further underscores the limitations of interpreting this value, but subgroup and meta-regression analyses allowed us to identify key patterns underlying this variability.

Subgroup analyses partially explained this heterogeneity, revealing substantial differences between avian families that highlight the influence of intrinsic ecological and behavioural traits. The high prevalence observed in Anatidae aligns with their established role as primary AIV reservoirs, likely driven by their gregarious behaviour, aquatic lifestyle, and dabbling feeding habits that facilitate faecal-oral transmission [3, 9,29].

Shorebird families such as Scolopacidae (sandpipers) and Charadriidae (plovers) exhibited lower overall prevalence, though with substantial within-group heterogeneity likely driven by seasonal and geographical differences. Wille et al. (2023) [30] reported that prevalence in

**Table 2**  
Pooled AIV prevalence estimates by migration behaviour and primary habitat (IUCN classification), with corresponding number of studies ( $k$ ), between-study variance ( $\tau^2$ ), and heterogeneity ( $I^2$ ).

|                            | $k$ | Prevalence (95% CI) | $\tau^2$ | $I^2$ | No. samples | No. positives |
|----------------------------|-----|---------------------|----------|-------|-------------|---------------|
| <b>Migration behaviour</b> |     |                     |          |       |             |               |
| Altitudinal migrants       | 5   | 0.00% [0.00–0.59%]  | 0.0000   | 0.0%  | 265         | 1             |
| Full migrants              | 181 | 5.07% [4.08–6.15%]  | 0.0237   | 99.7% | 747 201     | 58 977        |
| Nomadic                    | 6   | 5.02% [0.00–16.53%] | 0.0500   | 90.8% | 641         | 31            |
| Non-migrants               | 51  | 0.77% [0.18–1.62%]  | 0.0107   | 89.7% | 17 049      | 309           |
| <b>Habitat</b>             |     |                     |          |       |             |               |
| Freshwater                 | 178 | 5.40% [4.39–6.51%]  | 0.0233   | 99.7% | 728 768     | 58 961        |
| Marine                     | 42  | 0.47% [0.10–1.04%]  | 0.0048   | 86.2% | 19 410      | 202           |
| Terrestrial                | 39  | 0.45% [0.00–1.64%]  | 0.0191   | 88.8% | 16 978      | 155           |

long-distance migratory Scolopacidae was lowest upon arrival at non-breeding sites in Australia but increased later in the season, possibly due to environmental conditions more conducive to virus persistence. Similarly, Olsen et al. (2006) [9] observed higher prevalence in waders during spring migration in North America, highlighting their potential role in sustaining virus circulation during migratory periods.

The seasonal patterns identified in temperate regions — with prevalence peaking in autumn and reaching a minimum in spring — are consistent with the post-breeding increase in immunologically naïve juveniles and elevated contact rates during migration, followed by declining detection as population immunity rises [31,32].

Importantly, the meta-regression revealed that seasonality was strongly region-dependent. In Europe, the autumn peak matches evidence that infection risk increases when migrants arrive and mix with residents at staging and stopover sites [32,33]. In North America, the summer and early autumn peak corresponds to the staging period when bird densities and the proportion of susceptible hatch-year birds are greatest [34]. Northern Asia displayed a distinct spring peak, plausibly explained by northward migration concentrating birds at key stopover wetlands before reaching breeding grounds [35,36].

In tropical regions, the marked difference between dry and wet seasons supports the hypothesis that reduced water availability concentrates waterbirds at remaining wetlands, increasing contact rates and facilitating faecal-oral virus transmission [37]. However, data from tropical regions remain limited, and further targeted surveillance is needed to confirm these patterns across different ecosystems.

Together, these regional differences highlight that seasonal AIV dynamics are shaped by flyway-specific factors, including the timing of migration, the geographic distribution of key wetland habitats, and local host community composition [9,38].

More broadly, surveillance intensity varies considerably across regions. Data from the Southern Hemisphere remain particularly sparse, and AIV circulation in South America was likely underestimated prior to the HPAI outbreaks detected since 2022 [39]. These geographical gaps limit comparability between regions and highlight the need to expand surveillance in under-sampled areas.

## 5. Limitations and potential sources of bias

This meta-analysis is subject to several limitations. First, the screening and selection of studies was conducted by a single author, which introduces a potential risk of selection bias. To mitigate this, title and abstract screening was performed twice by the same reviewer, and all full texts were evaluated using predefined, quantitative eligibility criteria based on extractable detection data. Nevertheless, we acknowledge that independent duplicate screening would have provided stronger protection against selection bias.

Another important consideration is the interpretation of the pooled estimate. As discussed earlier, we defined and explicitly used the term *prevalence of sampled birds*, recognising that most underlying studies rely on opportunistic sampling rather than population-based sampling. These values do not reflect the true prevalence in wild bird populations but rather the proportion of positives among sampled individuals. This

limitation is inherent to wildlife surveillance, where random sampling is rarely feasible due to logistical and ecological constraints. Nevertheless, these data remain valuable for identifying broad patterns and drivers of AIV circulation.

Furthermore, we did not differentiate between AIV subtypes, as this information was not consistently reported across all studies. While some studies provided subtype-specific data (e.g., H5, H7), many only reported overall AIV prevalence, preventing a detailed analysis of subtype distribution. Although we included outbreak-related time periods as moderators in the meta-regression, none of them reached statistical significance after adjustment for other covariates. This suggests that while clade 2.3.4.4b and other viral lineages emergences may have influenced prevalence, their effects could not be clearly isolated with the available data. Moreover, changes in surveillance priorities following HPAI emergence, such as shifts in sampling timing, location, or target host species, may have influenced detection patterns without necessarily reflecting changes in underlying infection prevalence.

Variability in diagnostic methods may also have affected our results. We included both RT-PCR and virus isolation in embryonated eggs as diagnostic methods for detecting AIV and determining the number of positive samples. Although both methods are widely used in avian influenza surveillance, they have differences in sensitivity and specificity [40,41], which could introduce variability in positivity rates.

The scope of covariates was also limited by what was consistently available across studies. Important variables such as host age, sex, exact sampling location, and habitat type were often missing or reported inconsistently, limiting our ability to assess their influence on AIV prevalence. We took account of sampling seasons, but the majority of studies did not report this information and were therefore excluded from part of the analysis.

In addition to methodological limitations, several forms of bias may influence patterns observed in global AIV surveillance. Publication bias is difficult to rule out entirely. Although funnel plots and Egger's regression test did not provide statistical evidence of small-study effects, studies with exclusively negative results, particularly small-scale ones, may be less likely to be published, whereas studies reporting positive or unusually high prevalence may be preferentially disseminated.

Sampling bias is another important consideration. Our analyses did not find systematic associations between sampling intensity and species abundance or migratory behaviour, yet surveillance effort is likely influenced by factors not captured in our dataset. Researchers may preferentially re-sample species, locations, or time periods where AIV was previously detected, while species that are difficult to capture may remain underrepresented. Furthermore, the emergence of HPAI viruses has likely shifted surveillance priorities toward outbreak timing, locations close to poultry introductions, and species affected by mortality events. Such preferential sampling could influence apparent host or regional patterns independently of true infection dynamics.

## 6. Conclusions

This meta-analysis provides a comprehensive overview of AIV prevalence in sampled wild birds, based on existing literature. However, the

findings must be interpreted with caution given the high heterogeneity and the reliance on opportunistic sampling in most studies. While these limitations constrain the generalisability of the pooled estimates, the meta-analysis still highlights consistent patterns and identifies key factors driving infection detection. Future surveillance studies could draw on this study to improve comparability between regions, species and seasons through harmonised sampling designs and standardised metadata reporting.

### CRedit authorship contribution statement

**Marie-Cécile Dupas:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Alessandra Falcucci:** Writing – review & editing, Project administration. **Claudia Pittiglio:** Writing – review & editing, Project administration. **Xavier Roche:** Writing – review & editing, Project administration. **Giuseppina Cinardi:** Writing – review & editing. **Amy Delgado:** Writing – review & editing. **Ismaila Seck:** Writing – review & editing, Supervision, Project administration, Funding acquisition. **Madhur Dhingra:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Marius Gilbert:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

### Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Marie-Cecile Dupas reports financial support was provided by Food and Agriculture Organisation of the United Nations. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Acknowledgment

MCD is supported by the BELSPO project BE-PIN. MCD acknowledges funding from the Food and Agriculture Organisation of the United Nations (FAO).

### Appendix A. Supplementary data

Supplementary material related to this article can be found online at <https://doi.org/10.1016/j.onehlt.2026.101338>. Description of each Material is given in Document S1.

### Data availability

The data are available in the supplementary materials.

### References

- [1] D.J. Alexander, An overview of the epidemiology of avian influenza, *Vaccine* 25 (30) (2007) 5637–5644.
- [2] L. Clark, J. Hall, Avian influenza in wild birds: status as reservoirs, and risks to humans and agriculture, in: *Ornithological Monographs*, 2006, pp. 3–29.
- [3] D.E. Stallknecht, J.D. Brown, Ecology of avian influenza in wild birds, *Avian Influenza* (2008) 43–58.
- [4] B.A. Hanson, D.E. Stallknecht, D.E. Swayne, L.A. Lewis, D.A. Senne, Avian influenza viruses in Minnesota ducks during 1998–2000, *Avian Diseases* 47 (s3) (2003) 867–871.
- [5] S. Krauss, D. Walker, S. Paul Pryor, et al., Influenza A viruses of migrating wild aquatic birds in North America, *Vector-Borne Zoonotic Dis.* 4 (3) (2004) 177–189.
- [6] R.G. Webster, W.J. Bean, O.T. Gorman, T.M. Chambers, Y. Kawaoka, Evolution and ecology of influenza A viruses, *Microbiol. Rev.* 56 (1) (1992) 152–179.
- [7] J.A. Giacinti, A.V. Signore, M.E.B. Jones, et al., Avian influenza viruses in wild birds in Canada following incursions of highly pathogenic H5N1 virus from Eurasia in 2021–2022, *MBio* 15 (8) (2024) e03203–e03223.

- [8] E. Ntakiyisumba, S. Lee, B.-Y. Park, H.-J. Tae, G. Won, Prevalence, seroprevalence and risk factors of avian influenza in wild bird populations in Korea: A systematic review and meta-analysis, *Viruses* 15 (2) (2023) 472.
- [9] B. Olsen, V.J. Munster, A. Wallensten, J. Waldenstrom, A.D.M.E. Osterhaus, R.A.M. Fouchier, Global patterns of influenza A virus in wild birds, *Science* 312 (5772) (2006) 384–388.
- [10] V.J. Munster, R.A.M. Fouchier, Avian influenza virus: of virus and bird ecology, *Vaccine* 27 (45) (2009) 6340–6344.
- [11] L.Z. Garamszegi, A.P. Moller, Prevalence of avian influenza and host ecology, *Proc. R. Soc. B: Biological Sci.* 274 (1621) (2007) 2003–2012.
- [12] D.K. Bonilla-Aldana, Y. Holguin-Rivera, I. Cortes-Bonilla, et al., Prevalence of avian influenza H5N6 in birds: A systematic review and meta-analysis of other viral zoonosis, *World's Vet. J.* (2) (2021) 146–156.
- [13] D.M. Calle-Hernández, V. Hoyos-Salazar, D.K. Bonilla-Aldana, Prevalence of the H5n8 influenza virus in birds: Systematic review with meta-analysis, *Travel. Med. Infect. Dis.* 51 (2023) 102490.
- [14] X.-Y. Yang, Q.-L. Gong, Y.-J. Li, et al., The global prevalence of highly pathogenic avian influenza A (h5n8) infection in birds: A systematic review and meta-analysis, *Microb. Pathog.* 176 (2023) 106001.
- [15] W.-X. Tan, S.-Y. Qin, X. Yang, et al., Global prevalence and distribution of H9 subtype of avian influenza viruses in wild birds: Literature review with meta-analysis, *Vector-Borne Zoonotic Dis.* 25 (5) (2025) 346–358.
- [16] X. Chen, C. Li, H.-T. Sun, J. Ma, Y. Qi, S.-Y. Qin, Prevalence of avian influenza viruses and their associated antibodies in wild birds in China: A systematic review and meta-analysis, *Microb. Pathog.* 135 (2019) 103613.
- [17] The R Development Core Team, The R project for statistical computing, 2008, <http://www.r-project.org>.
- [18] W. Viechtbauer, Conducting meta-analyses in R with the metafor package, *J. Stat. Softw.* 36 (3) (2010) 1–48.
- [19] S. Tarr, I. Townsend, Iucnredlist: An R package for the IUCN red list API, R package version 0.1, 2025, URL: <https://github.com/IUCN-UK/iucnredlist>.
- [20] M. Egger, G.D. Smith, M. Schneider, C. Minder, Bias in meta-analysis detected by a simple, graphical test, *BMJ* 315 (7109) (1997) 629–634.
- [21] W.H. Kruskal, W.A. Wallis, Use of ranks in one-criterion variance analysis, *J. Amer. Statist. Assoc.* 47 (260) (1952) 583–621.
- [22] O.J. Dunn, Multiple comparisons using rank sums, *Technometrics* 6 (3) (1964) 241–252.
- [23] A. Signorell, K. Aho, A. Alfons, et al., DescTools: Tools for descriptive statistics. R package version 0.99.18, in: R Foundation for Statistical Computing, Vienna, Austria, 2016.
- [24] J.P.T. Higgins, S.G. Thompson, Quantifying heterogeneity in a meta-analysis, *Stat. Med.* 21 (11) (2002) 1539–1558.
- [25] M.J. Page, J.E. McKenzie, P.M. Bossuyt, et al., The PRISMA 2020 statement: an updated guideline for reporting systematic reviews, *BMJ* 372 (2021).
- [26] Y. Si, A.K. Skidmore, T. Wang, et al., Spatio-temporal dynamics of global H5N1 outbreaks match bird migration patterns, *Geospatial Health* 4 (1) (2009) 65–78.
- [27] Global Consortium for H5N8 and Related Influenza Viruses, Role for migratory wild birds in the global spread of avian influenza H5N8, *Science* 354 (6309) (2016) 213–217.
- [28] R. Xie, K.M. Edwards, M. Wille, et al., The episodic resurgence of highly pathogenic avian influenza H5 virus, *Nature* 622 (7984) (2023) 810–817.
- [29] K.J. Vandegrift, S.H. Sokolow, P. Daszak, A.M. Kilpatrick, Ecology of avian influenza viruses in a changing world, *Ann. New York Acad. Sci.* 1195 (1) (2010) 113–128.
- [30] M. Wille, S. Lisovski, D. Roshier, et al., Strong host phylogenetic and ecological effects on host competency for avian influenza in Australian wild birds, *Proc. R. Soc. B* 290 (1991) 20222237, 2023.
- [31] V.J. Munster, C. Baas, P. Lexmond, et al., Spatial, temporal, and species variation in prevalence of influenza A viruses in wild migratory birds, *PLoS Pathog.* 3 (5) (2007) e61.
- [32] J.G.B. van Dijk, B.J. Hoyer, J.H. Verhagen, B.A. Nolet, R.A.M. Fouchier, M. Klaassen, Juveniles and migrants as drivers for seasonal epizootics of avian influenza virus, *J. Anim. Ecol.* 83 (1) (2014) 266–275.
- [33] N.S. Lewis, Z. Javakhishvili, C.A. Russell, A. Machabishvili, P. Lexmond, J.H. Verhagen, O. Vuong, T. Onashvili, M. Donduashvili, D.J. Smith, et al., Avian influenza virus surveillance in wild birds in Georgia: 2009–2011, *PLoS One* 8 (3) (2013) e58534.
- [34] R. Nallar, Z. Papp, T. Epp, et al., Demographic and spatiotemporal patterns of avian influenza infection at the continental scale, and in relation to annual life cycle of a migratory host, *PLoS One* 10 (6) (2015) e0130662.
- [35] D.J. Prosser, P. Cui, J.Y. Takekawa, M. Tang, Y. Hou, B.M. Collins, B. Yan, N.J. Hill, T. Li, Y. Li, et al., Wild bird migration across the Qinghai-Tibetan plateau: a transmission route for highly pathogenic H5N1, *PLoS One* 6 (3) (2011) e17622.
- [36] H. Tian, S. Zhou, L. Dong, T.P. van Boeckel, Y. Cui, S.H. Newman, J.Y. Takekawa, D.J. Prosser, X. Xiao, Y. Wu, et al., Avian influenza H5N1 viral and bird migration networks in Asia, *Proc. Natl. Acad. Sci.* 112 (1) (2015) 172–177.
- [37] X. Wang, X. Xiao, C. Zhang, J. Dong, B. Li, Effects of the 2022 extreme droughts on avian influenza transmission risk in Poyang Lake, *Innov. Life* 1 (3) (2023) 100044.
- [38] Z. Hubálek, An annotated checklist of pathogenic microorganisms associated with migratory birds, *J. Wildl. Dis.* 40 (4) (2004) 639–659.

- [39] M. Leguía, A. García-Glaessner, B. Muñoz-Saavedra, et al., Highly pathogenic avian influenza A (H5N1) in marine mammals and seabirds in Peru, *Nat. Commun.* 14 (1) (2023) 5489.
- [40] E. Spackman, D.A. Senne, L.L. Bulaga, et al., Development of real-time RT-PCR for the detection of avian influenza virus, *Avian Dis.* 47 (s3) (2003) 1079–1082.
- [41] M.B. Shabat, R. Meir, R. Haddas, et al., Development of a real-time TaqMan RT-PCR assay for the detection of H9N2 avian influenza viruses, *J. Virol. Methods* 168 (1–2) (2010) 72–77.