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Phylodynamic approaches to studying avian influenza virus

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ABSTRACT

Avian influenza viruses can cause severe disease in domestic and wild birds and are a pandemic threat. Phylodynamics is the study of how epidemiological, evolutionary, and immunological processes can interact to shape viral phylogenies. This review summarizes how phylodynamic methods have and could contribute to the study of avian influenza viruses. Specifically, we assess how phylodynamics can be used to examine viral spread within and between wild or domestic bird populations at various geographical scales, identify factors associated with virus dispersal, and determine the order and timing of virus lineage movement between geographic regions or poultry production systems. We discuss factors that can complicate the interpretation of phylodynamic results and identify how future methodological developments could contribute to improved control of the virus.

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Background

Avian influenza viruses (AIVs) pose a considerable risk to human and animal health (Mostafa *et al.*, 2018; Lycett *et al.*, 2019; Rimi *et al.*, 2019). These viruses belong to the species *Alphainfluenzavirus influenzae* (previously known as Influenza A virus (IAV)) (Lefkowitz *et al.*, 2018; ICTV, 2022), and have single-stranded, negative-sense, and eight-segmented RNA genomes (Seiler *et al.*, 2018; Rimi *et al.*, 2019; Wille & Holmes, 2020). AIVs are subtyped into "HxNy" based on the antigenicity and genetic diversity of the two surface glycoproteins: haemagglutinin (H1 – H16 in birds) and neuraminidase (N1 – N9 in birds) (Yoon *et al.*, 2014; Blaurock *et al.*, 2020; Verhagen, Eriksson, *et al.*, 2021). Wild aquatic birds, particularly Anseriformes (e.g. geese, ducks) and Charadriiformes (e.g. gulls, shorebirds), are the primary reservoirs of AIVs (Olsen *et al.*, 2006). However, AIVs can spill over to cause sporadic infection or sustained transmission within domestic avian hosts (Mostafa *et al.*, 2018; Lycett *et al.*, 2019). We can categorize viruses as low pathogenic avian influenza viruses (LPAIVs) and highly pathogenic avian influenza viruses (HPAIVs) based on their pathogenicity in chickens and the presence of insertions in the HA cleavage site (More *et al.*, 2017). LPAIVs cause asymptomatic infection or mild disease in domestic birds, thereby harming the poultry industry via decreased egg or meat production, higher vaccination expenses, and trade restrictions (Busani *et al.*, 2007; Gonzales *et al.*, 2021; Ripa *et al.*, 2021). Only LPAIVs of H5 and H7 subtypes are known to evolve into HPAIVs, a process that involves the insertion of multiple basic amino acids in the HA cleavage site (Rott, 1992; Alexander, 2007). HPAIVs cause severe disease and fatalities in both domestic birds (Verhagen *et al.*, 2014; Nuñez & Ross, 2019) and wild birds, respectively harming the economy and conservation efforts (Kleyheeg *et al.*, 2017; Banyard *et al.*, 2022; Lean *et al.*, 2022). Several AIV strains can also infect humans and other mammalian species (e.g. swine, seals) and, thus, pose a potential pandemic threat (Ren *et al.*, 2016; Nuñez & Ross, 2019; Blagodatski *et al.*, 2021; Agüero *et al.*, 2023; Puryear *et al.*, 2023; Vreman *et al.*, 2023).

Phylodynamics studies how epidemiological, immunological, and evolutionary processes shape viral genetic diversity. Approaches developed within this framework can help recover viral dispersal patterns and evolutionary processes, even when virus genomic data is sampled relatively sparsely from an infected population (Grenfell *et al.*, 2004; Volz *et al.*, 2013; Rife *et al.*, 2017). Time-scaled phylogenies can be inferred using molecular clock models, which quantify the rate of genetic change over time and therefore enable phylogenetic branch lengths to be expressed as units of time rather than as nucleotide substitutions per site (Drummond *et al.*, 2006; Pybus & Rambaut, 2009) (Box 1). RNA viruses,

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including AIVs, typically have exceptionally short generation times, high evolutionary rates, and large population sizes (Duffy, 2018; Wille & Holmes, 2020). Consequently, genetic substitutions in viral genomes often occur on similar time scales as transmission events between hosts. Hence, it is possible to reconstruct outbreak dynamics from time-scaled phylogenies, as they contain a "molecular footprint" of viral spread (Grenfell *et al.*, 2004; Lemey *et al.*, 2009; Pybus & Rambaut, 2009). When genome sampling location is available, we can use phylodynamic techniques to reconstruct the geographical distribution of viral lineages ("phylogeography"), thereby revealing valuable information about viral spread and factors associated with faster or more frequent viral lineage movement events (Lemey *et al.*, 2010; Faria *et al.*, 2011; Gill *et al.*, 2016).

The most common tools for phylodynamic analyses employ a Bayesian Markov Chain Monte Carlo (MCMC) framework to efficiently explore highly complex models involving many different parameters (Drummond & Rambaut, 2007; Bouckaert *et al.*, 2014). A Bayesian framework has several advantages compared to the maximum likelihood or parsimony-based approaches. Firstly, Bayesian approaches allow for the incorporation of multiple sources of data or prior knowledge (e.g. divergence times, substitution rates) (Alfaro & Holder, 2006; Baele *et al.*, 2017; Chakraborty *et al.*, 2021). Perhaps more importantly, such approaches generate posterior distributions of phylogenetic trees, thus allowing uncertainty in parameter estimates to be captured (this has been reviewed extensively elsewhere, (e.g. Faria *et al.*, 2011; Volz *et al.*, 2013; Gill *et al.*, 2016; Rasmussen & Grünwald, 2020; Dellicour *et al.*, 2021). Maximum likelihood (ML)-based methods are more limited in scope of possible analyses, but are often less computationally intensive than the more popular Bayesian approaches (Baele *et al.*, 2018; Sagulenko *et al.*, 2018; Ishikawa *et al.*, 2019). This can be beneficial when dealing with large datasets, limited computed resources, or when faster but lower complexity models are appropriate to inform emergency responses. Such ML phylodynamic methods typically use a single ML tree, enabling faster time-to-answer compared to Bayesian phylodynamic inference.

Recent trending decreases in the cost and time required to generate and analyse virus genetic data have led to rapid innovation within the field of phylodynamics and a subsequent increase in popularity (Gill *et al.*, 2016; Rife *et al.*, 2017; Grubaugh *et al.*, 2019; Cardona-Ospina *et al.*, 2021). This review highlights how phylodynamic methods have and may continue to aid the study of AIV spatiotemporal dispersal. We first explore recent studies that use phylodynamics to infer AIV dispersal dynamics within or between wild birds and domestic poultry populations at various geographical scales and discuss factors that can complicate the generation of reliable conclusions. Specifically, we discuss the inference of factors associated with AIV transmission, the order and timing of transmission and lineage dispersal events during an outbreak, and how viral lineages can move between different regions and sectors of poultry production systems. We then consider future challenges and opportunities for using phylodynamic approaches within AIV research.

Wild bird populations

Tracing viral incursions

Phylodynamics has helped identify global movements of AIV lineages in wild bird populations (Baele *et al.*, 2018; Zhang *et al.*, 2023). Many studies have used time-calibrated phylogenies (Box 1) to estimate the sampling time and location of unobserved viral ancestors, and hence reconstruct the timings and origins of viral (particularly HPAIV) incursions into different wild bird populations (e.g. Lee *et al.*, 2018; Hill *et al.*, 2019; Zhang, Fan *et al.*, 2020; Beerens *et al.*, 2021; Liang, Krog, *et al.*, 2021; Xie *et al.*, 2022). For instance, one study showed that HPAIV H5N8 infections in wild birds present in the Netherlands in late 2020 were likely introductions from wild birds in Egypt and not elsewhere in Europe, as was anticipated based on proximity (Beerens *et al.*, 2021). This finding demonstrates how phylogenetic approaches can provide information on AIV spread that might not be detectable using standard epidemiological analyses based on reported cases.

Complications in interpreting where virus lineages originate can arise in instances where gene segments from multiple genetically diverse AIVs reassort during co-infection (Araujo *et al.*, 2018; Wille & Holmes, 2020; Verhagen, Fouchier *et al.*, 2021). Gene segments acquired from each different parent virus typically require analysis using separate phylogenies to capture the different evolutionary histories of each parent lineage (Lu *et al.*, 2014). Accordingly, reassortant sequences are sometimes represented using a phylogenetic network instead of a single tree (Frost *et al.*, 2015; Stolz *et al.*, 2022) or, more commonly, removed, with only one gene segment (usually haemagglutinin (HA) (Heaton *et al.*, 2013)) selected for analyses. The latter approach limits our understanding of AIV diffusion (Lu *et al.*, 2014; Parvin *et al.*, 2014; Frost *et al.*, 2015; Venkatesh *et al.*, 2018). Although reassortant sequences could perhaps be better accommodated in AIV phylodynamic analyses using a similar approach to that detailed in Müller *et al.*, (2020), which was used to explicitly infer reassortment rates in different human influenza virus lineages, the complexity of this method likely prevents it being used widely (Müller *et al.*, 2020).

Geographic structuring of genetic diversity

Phylodynamic methods have been used to investigate whether AIV lineages found in wild birds are structured according to avian flyways and host ecology (Hurt *et al.*, 2014; Araujo *et al.*, 2018; Mine *et al.*, 2019; Sharshov *et al.*, 2019; Verhagen *et al.*, 2020; Zhang *et al.*, 2023). Several studies indicate that avian hosts within geographically isolated regions sometimes harbour AIV segment lineages that are seemingly relatively distinct from other sampled lineages circulating globally (Hansbro *et al.*, 2010; Hurt *et al.*, 2014; Araujo *et al.*, 2018; Wille *et al.*, 2022). For instance, one study detected an H11N2 lineage in Adélie penguins (*Pygoscelis adeliae*) in Antarctica in 2013 that likely diverged approximately between the 1960s-1980s from the most closely related AIV sequences worldwide (Hurt *et al.*, 2014). However, it is difficult to determine whether these findings represent true lineage geographic isolation or if lineages only appear geographically structured due to a scarcity of samples from nearby locations that may nevertheless be epidemiologically linked (e.g. southern Chile, Argentina). Other analyses reveal that AIV lineages can be shared between distant regions (Bahl *et al.*, 2009; zu Dohna *et al.*, 2009; Mine *et al.*, 2019; Sharshov *et al.*, 2019; Verhagen *et al.*, 2020; Caliendo *et al.*, 2022). For instance, recent discrete phylogeographic analyses (Box 1) based on the neuraminidase (NA) indicated likely intercontinental AIV dispersal between North America and Eurasia (Mine *et al.*, 2019).

Box 1.

Viral phylogeography is the reconstruction of viral movement between geographic locations using virus genetic sequences. Phylogeographic approaches can be categorized based on whether the modelled locations are discrete (e.g. country, administrative district) or continuous (geographic coordinates) (Lemey *et al.*, 2009; Faria *et al.*, 2011).

Discrete trait analyses are sometimes used out of necessity, for instance, when precise geographic sampling coordinates are unavailable (De Maio *et al.*, 2015; Hill *et al.*, 2015; Lycett *et al.*, 2019). However, these approaches are usefully applied when sequences cluster naturally by geographic location because viral movement is affected by geographical (e.g. oceans, mountains) and/or political (e.g. borders) barriers (Alkhamis *et al.*, 2015; De Maio *et al.*, 2015; Zhang, Chen *et al.*, 2020). Several software packages (e.g. TreeTime (Sagulenko *et al.*, 2018), PastML (Ishikawa *et al.*, 2019)) have been developed that enable reconstruction of ancestral characters within a maximum-likelihood framework. The most commonly used software packages for phylodynamic inference, BEAST (Drummond & Rambaut, 2007) and BEAST2 (Bouckaert *et al.*, 2014), rely on a Bayesian inference framework and offer several different approaches for phylogeography using discrete traits. We summarize different maximum likelihood and Bayesian approaches below.

Maximum likelihood ancestral character reconstruction: Maximum likelihood approaches can also be used to estimate the most likely states of discrete traits (e.g. which country or host species) at internal nodes of phylogenies (Cunningham *et al.*, 1998; Schmidt & von Haeseler, 2009; Hadfield *et al.*, 2018; Sagulenko *et al.*, 2018; Ishikawa *et al.*, 2019). These approaches focus on first estimating the most likely phylogeny given the data (i.e. the maximum likelihood tree), and then estimating the most likely history of discrete states at each node (Cunningham *et al.*, 1998; Schmidt & von Haeseler, 2009; Sagulenko *et al.*, 2018; Ishikawa *et al.*, 2019). Branch length or evolutionary time is accounted for, such that geographic movements are more likely to occur on longer branches. This is in contrast to Bayesian approaches implemented in BEAST and BEAST2, which estimate the history of discrete traits for each tree in the posterior tree distribution and hence can more fully account for phylogenetic uncertainty but as a result can be significantly slower (Faria *et al.*, 2011; Volz *et al.*, 2013; Gill *et al.*, 2016; Dellicour *et al.*, 2021).

Discrete trait analysis: In one common approach (often known as "discrete trait analysis", whilst being only one of several approaches for phylogeographic inference using discrete traits), phylogenetic branch locations are estimated using continuous-time Markov chains, i.e. modelled as moving instantaneously at specific rates between a fixed number of discrete locations (Lemey *et al.*, 2009; Faria *et al.*, 2011). (Figure 1A). A frequently applied extension of this model known as **Bayesian stochastic search variable selection (BSSVS)** attempts to limit the number of possible recovered transitions between pairs of locations to those that adequately explain the phylogenetic diffusion process (Lemey *et al.*, 2009). Biased sampling can affect the statistical inference of discrete trait analyses as the relative sampling intensities of different discrete locations or traits affect the estimates of viral movements (De Maio *et al.*, 2015; Layan *et al.*, 2023).

Structured coalescent approaches: Structured coalescent approaches, including those implemented in MASCOT (Müller *et al.*, 2018) and BASTA (De Maio *et al.*, 2015) within BEAST 2, explicitly model ancestry within and movement between discrete subpopulations, known as "demes" (Figure 1A) (Vaughan *et al.*, 2014; De Maio *et al.*, 2015; Müller *et al.*, 2018). These methods can be less susceptible to sampling bias than classical coalescent models in certain instances (De Maio *et al.*, 2015; Müller *et al.*, 2018; Layan *et al.*, 2023). However, structured coalescent phylogeographic models are typically more computationally demanding than discrete trait phylogeographic models, and thus are mostly applied to small numbers of demes (De Maio *et al.*, 2015; Müller *et al.*, 2018; Layan *et al.*, 2023). Additionally, although population size can vary between demes, structured coalescent models assume that virus population size in each deme remains constant, which may be less appropriate for investigating AIV lineage expansions in naïve host populations or AIVs with strong seasonality in transmission (De Maio *et al.*, 2015; Layan *et al.*, 2023). Both discrete trait analyses and structured coalescent approaches can be used to model virus movement between other discrete traits (Faria *et al.*, 2011; De Maio *et al.*, 2015), such as host species (Figure 1B) (Ren *et al.*, 2016; Hicks *et al.*, 2020). Furthermore, generalized linear model (GLM) extensions of these methods (Lemey *et al.*, 2012, 2014; Faria *et al.*, 2013; Müller *et al.*, 2019) can be used to evaluate covariates of virus movement, such as avian host density at each location or geographic distance between pairs of locations.

Multitype birth–death models: Like structured coalescent approaches, multitype birth–death (MTBD) models (e.g. as implemented in the BEAST 2 package bdmm (Kühnert *et al.*, 2016)) are able to explicitly model transmission within structured populations, and represent an extension of the birth–death models described in Box 2. MTBD models involve the estimation of time-varying "birth" rates (transmission rate), "death" rates (rate of becoming non-infectious or death) for each of several discrete subpopulations, and "per-lineage migration rate" (changes in the subpopulation of an individual due to migration) (FitzJohn, 2012; Stadler & Bonhoeffer, 2013; Kühnert *et al.*, 2016; Barido-Sottani *et al.*, 2020). Unlike the structured coalescent approaches, which assume a constant population size within demes, the MTBD allows for population size to change through time (Stadler *et al.*, 2015; Seidel *et al.*, 2020).

Continuous phylogeography: In the continuous phylogeographic model, virus lineage movement is modelled between geographical coordinates (e.g. latitude and longitude) (Figure 1C & D) (Lemey *et al.*, 2009, 2010). Virus lineage movement is most commonly modelled using a relaxed random walk model (Lemey *et al.*, 2010), which allows the rate of viral dispersal to vary across the phylogeny. To evaluate spatiotemporal covariates associated with virus dispersal route or velocity, we can conduct *post-hoc* analysis using the R package "*seraphim*" (Dellicour *et al.*, 2016).

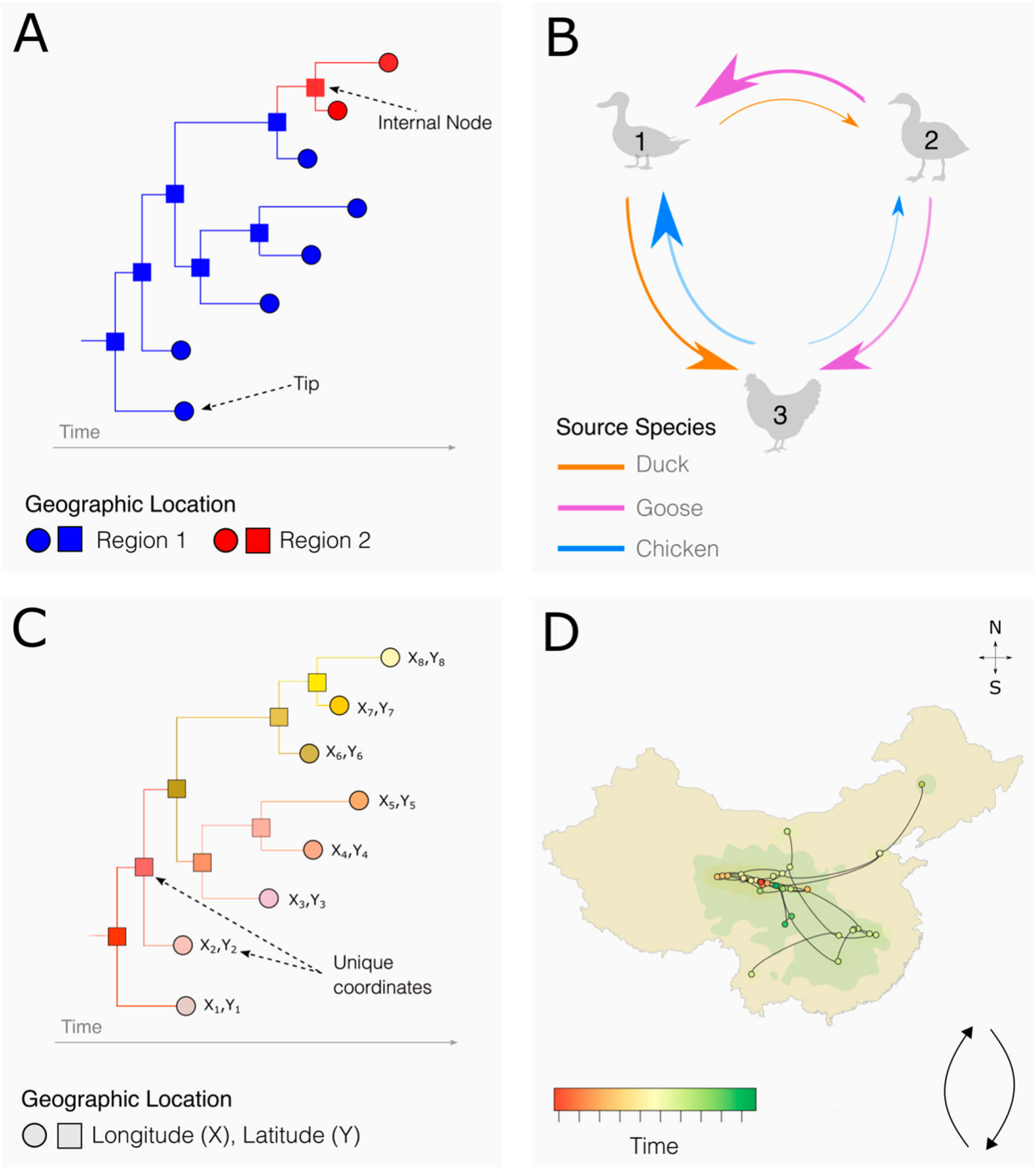

Figure 1. Conceptual representation of common phylogeographic methods. A: Time-calibrated phylogeny estimated with a phylogeographic model with discrete traits. The inferred locations of the ancestral internal nodes (squares) are estimated from the set of discrete locations predefined at the tips (i.e. locations of sampled sequences; circles). B: Discrete trait (e.g. location or host species) analysis. Here, arrows indicate statistically significant virus lineage transitions between bird types. Arrow thickness corresponds to the inferred viral flow rate. C: Time-calibrated phylogeny estimated with continuous phylogeographic inference. The inferred geographic coordinates of the internal nodes (i.e. unsampled virus ancestor) can differ from the geographical sampling coordinates of the sequences at the tips. Both internal nodes and tips are coloured by location. D: Continuous phylogeographic reconstruction using information contained in estimated phylogenies such as C, in which the dots represent the internal and external nodes of the time-scaled phylogeny, coloured according to time. The curvature direction of the lines between dots indicates the inferred direction of viral movement. Coloured polygons represent the statistical uncertainty of the inferred internal node locations, which is derived from a posterior tree distribution.

Sampling biases (i.e. disproportionate sampling of virus genomes compared to true infection prevalence) can strongly impact phylogeographic analyses, with under-sampled locations more likely to be inferred as sinks when using discrete trait approaches (De Maio *et al.*, 2015; Kalkauskas *et al.*, 2021; Layan *et al.*, 2023). The international spread of AIV has been predominately inferred from virus genetic data

collected in North America and northern Europe (Hill *et al.*, 2022). Wild bird sampling remains relatively limited in several areas of Central and South America, Africa, the Middle East, and polar regions, which may result in these regions being overestimated as sink locations for virus lineages (Hurt *et al.*, 2014; Araujo *et al.*, 2018; Fusaro *et al.*, 2019; Naguib *et al.*, 2019; Kalonda *et al.*, 2020; Hill *et al.*, 2021; Lo *et al.*, 2022). Accordingly, phylodynamic investigations of the global spread of AIV would benefit from increased AIV genomic surveillance in undersampled locations and host species.

Migratory flyways and mixing zones

Over 50 billion birds are estimated to migrate annually, with most flyways linking breeding grounds at high latitudes and over-wintering sites at low latitudes (Boere *et al.*, 2006; Bahl *et al.*, 2013). Several different phylodynamic studies using discrete trait analyses (Box 1) report that AIV lineage movement rates are greater within flyways than between flyways in Asia (Central Asian, East Asian) (Tian, Zhou, *et al.*, 2015) and in North America (Central, Mississippi, Atlantic) (Scotch *et al.*, 2014; Fries *et al.*, 2015; Li *et al.*, 2018). Continuous phylogeographic analyses (Box 1), in which virus lineage movement is modelled as a diffusion process between geographical coordinates (Lemey *et al.*, 2009, 2010), demonstrated that H5N1 movement throughout Asia and Russia (1996–2011) correlates with the geographical extent of known flyways (Trovão *et al.*, 2015). While a crude simplification to capture avian movement trends, "flyways" appear a crucial facilitator of long-distance AIV spread in wild birds.

Several studies indicate that AIV transmission between birds during congregation at breeding grounds or staging areas where multiple flyways overlap ("mixing zones") may shape the subsequent global dissemination of AIV lineages (Ramey *et al.*, 2010; Gerloff *et al.*, 2013; Huang *et al.*, 2014; Lee *et al.*, 2015; Venkatesh *et al.*, 2018; Mine *et al.*, 2019; Gass *et al.*, 2023). For example, Mine *et al.* (2019) determined that AIVs sampled in mixing zones in Mongolia and Siberia from wild birds that use different flyways were often phylogenetically intermixed. The study used the Bayesian tip-association significance testing (BaTS) software, which implements *post-hoc* statistical tests on time-calibrated trees to determine if sequences significantly cluster by a trait, such as sampling location. This approach enables rapid assessment of whether viral genetic diversity at tree tips is geographically structured, but, unlike discrete or continuous phylogeographic approaches, cannot be used to estimate full histories of virus lineage movement. The above-mentioned phylogenetic clustering patterns reported in Mine *et al.* (2019) are consistent with birds sharing AIVs in mixing zones before dissemination along different flyways, hence enabling long-distance diffusion of viral lineages between multiple continents or regions (Mine *et al.*, 2019). Consequently, the authors hypothesized that cross-flyway viral diffusion may have contributed to the simultaneous outbreaks of H5N6 HPAIVs in East Asia and Europe in 2017–2018 (Mine *et al.*, 2019). Similar findings have been observed in mixing zones in the Nile Delta and the Republic of Georgia (Gerloff *et al.*, 2013; Venkatesh *et al.*, 2018).

Several phylodynamic studies have shown high AIV genetic diversity in some mixing zones (Ramey *et al.*, 2010; Gerloff *et al.*, 2013; Venkatesh *et al.*, 2018, 2020; Mine *et al.*, 2019). High-density congregation of wild birds associated with different flyways at mixing zones may provide ideal conditions for AIV reassortment by increasing the probability of co-infections with diverse genotypes and subtypes (Venkatesh *et al.*, 2018; Mine *et al.*, 2019). However, further research is required to robustly determine if reassortant AIV genotypes exist at higher frequencies in mixing zones than in non-mixing zones. While phylodynamic approaches have been valuable in demonstrating the role of flyways and mixing zones in structuring AIV dispersal and reassortment patterns, several challenges remain. The scarcity of both wild bird migration data and wild bird sampling in some regions (particularly low- and middle-income countries) limits our ability to fully characterize how migratory flyways impact AIV dispersal patterns globally (Takekawa *et al.*, 2010; Palm *et al.*, 2015; Tian, Zhou, *et al.*, 2015; Fusaro *et al.*, 2019; Mine *et al.*, 2019; Yong *et al.*, 2021; Zhang *et al.*, 2023). Secondly, using environmental and flyway data averaged over months or years limits our ability to understand the impacts of changes in weather or environmental conditions on wild bird-mediated AIV dispersal patterns (Kirby *et al.*, 2008; Vandegrift *et al.*, 2010; Iwamura *et al.*, 2013; Bahl *et al.*, 2016; Sullivan *et al.*, 2018).

Roles of different host taxa

Several studies employing phylodynamic methods demonstrate how movement variation between wild birds from different taxonomic orders might impact AIV dispersal patterns (Ramey *et al.*, 2010; Miller *et al.*, 2011; Wille *et al.*, 2011; Hall *et al.*, 2013; Hill *et al.*, 2022; Gass *et al.*, 2023). In the boreal and temperate territories of the Northern Hemisphere, migratory Charadriiformes (e.g. shorebirds, gulls) are more abundant and undertake long-distance migrations across oceans more frequently than migratory Anseriformes (e.g. ducks, geese)

(Ramey *et al.*, 2010; Miller *et al.*, 2011; Wille *et al.*, 2011; Hall *et al.*, 2013; Hill *et al.*, 2022; Gass *et al.*, 2023). Consequently, it has been suggested that Charadriiformes may facilitate intercontinental AIV transmission in these areas more than Anseriformes (Cappelle *et al.*, 2012; Gaidet *et al.*, 2012; Gaidet, 2016; Rimondi *et al.*, 2018; Hoye *et al.*, 2021; Wille *et al.*, 2023). Phylodynamic support for this hypothesis exists in the seemingly more frequent detection of inter-hemispheric reassortment events between American and Eurasian lineages associated with Charadriiformes compared to Anseriformes (Bahl *et al.*, 2009; Ramey *et al.*, 2010; Wille *et al.*, 2011; Van Borm *et al.*, 2012; Hall *et al.*, 2013; Lang *et al.*, 2016). Conversely, in areas such as the tropical regions of West Africa, there is a high abundance of long-distance migratory Anseriformes but a low abundance of Charadriiformes migrants. There, Anseriformes are instead thought to be the primary drivers of virus movement between regions and continents (Cappelle *et al.*, 2012; Gaidet, 2016).

Discrete trait analyses (Box 1) have been used to explore how wild bird species with contrasting migration behaviours may differently influence AIV spread (Hill *et al.*, 2020, 2022). For instance, one study suggested that in Egypt and adjacent Black Sea-Mediterranean countries, local migrant species (common shelduck (*Tadorna tadorna*)) generally contributed to local AIV amplification, while longer distance migrants (northern shoveler (*Spatula clypeata*) and northern pintail (*Anas acuta*)) carried AIV lineages over longer distances (Hill *et al.*, 2020). Careful analyses and interpretation of results regarding the contribution of different species to AIV dispersal is critical because virus genome sequences are often biased towards hunted species (e.g. game birds) or those that are easily detected when they die (e.g. larger inland birds such as mute swans (*Cygnus olor*)) (Runstadler *et al.*, 2013; Lebarbenchon *et al.*, 2015; Bahl *et al.*, 2016; Beerens *et al.*, 2021; McBride *et al.*, 2021; Hill *et al.*, 2022). The existence of within-species variation in movement ecology, both between juveniles and adults (van Dijk *et al.*, 2014) and between resident and migratory populations from the same species (Lisovski *et al.*, 2018), further complicates generalization of host species traits associated with long-distance AIV spread.

Between wild and domestic birds

Frequency and timing of movement

AIVs are regularly transmitted between wild and domestic birds (Fusaro *et al.*, 2011; Lebarbenchon & Stallknecht, 2011; Bahl *et al.*, 2016; Nuñez & Ross, 2019). The relative frequency of viral cross-species transmission events can be estimated using phylodynamic tools such as Markov jumps counting in combination with discrete trait phylogeography (Minin & Suchard, 2008a, b; Faria *et al.*, 2011) (Box 1). Markov jump counting approaches enable the counting of the expected number of transitions between modelled discrete traits, such as country or host species, along phylogenetic branches (Minin & Suchard, 2008a, b; Faria *et al.*, 2011). For example, Markov jumps counting analyses were used to infer that North America, east and southeast Asia are hotspots for cross-species transmission between wild and domestic birds (Ren *et al.*, 2016). Likewise, one large study of a globally sampled H9 AIV dataset used both discrete trait analyses and Markov jump counting to identify spatial asymmetry in the geographical areas where wild-to-domestic and/or domestic-to-wild viral transmission most often occurred (Bahl *et al.*, 2016). These methods must be used cautiously because Markov jumps analyses are very sensitive to disproportionate sampling from each group relative to true virus prevalence (Layan *et al.*, 2023). This is particularly problematic for AIV, where genome sequences are almost always more frequently available from poultry relative to wild birds (Bahl *et al.*, 2016; Ren *et al.*, 2016; Yang, Xie *et al.*, 2019).

The relative rates of transmission between domestic and wild bird populations can also be investigated using structured coalescent approaches and multitype birth–death models, which may be less sensitive biased sampling (Box 1) (De Maio *et al.*, 2015; Grear *et al.*, 2017; Yang, Müller, *et al.*, 2019; Guinat *et al.*, 2022). Such methods can allow the transition rates between populations or demes to vary depending on the direction or estimate a single rate regardless of the directionality (De Maio *et al.*, 2015; Kühnert *et al.*, 2016; Müller *et al.*, 2018; Barido-Sottani *et al.*, 2020). One study of a 2014 HPAIV outbreak in North American domestic poultry, caused by wild bird lineage spillover, inferred that minimal viral movement had occurred between wild and domestic birds over the subsequent course of the domestic outbreak (Grear *et al.*, 2017). Furthermore, estimates of basic reproductive number (R_0; the expected number of susceptible individuals in a naïve population infected by one infected host – see Box 2) indicated that the poultry outbreak size was stable ($R_0 \approx 1$) (Grear *et al.*, 2017). Taken together, these findings suggested that the poultry outbreak was largely self-sustaining (Grear *et al.*, 2017).

Several studies indicate that AIV transmission between wild and domestic birds can vary seasonally (Alarcon *et al.*, 2018; Ferenczi *et al.*, 2021; Gonzales *et al.*, 2021; Zhang *et al.*, 2021; Liang, Nissen, *et al.*, 2021). Recurrent temporal peaks in cross-species transmission events can be

investigated using phylodynamic tools that infer population demographic history (Frost & Volz, 2010; Karcher *et al.*, 2020) (Box 2). For example, one study observed that the effective population size of clade 2.3.4.4b H5N8 viruses in Chinese poultry, as estimated by a skyride coalescent model (Gill *et al.*, 2013) (Box 2), increased during winter 2020/21, as previously observed for H5 lineages/clades during winter 2013/14 and 2016/17 (Zhang *et al.*, 2021). Seasonal increases in viral effective population size and other phylogenetic evidence, such as estimated dates of incursion of new lineages, were interpreted as consistent with immigrating wild birds recurrently introducing new H5 viruses into domestic poultry (Zhang *et al.*, 2021).

Box 2.

Past population dynamics can be estimated through phylodynamic inference by analysing how virus **effective population size** ($\mathbf{N_e}$) changes over time. Briefly, the effective population size represents the size of an idealized viral outbreak (i.e. one without selection or population structure) that experiences the same level of genetic drift as the studied population (Magiorkinis *et al.*, 2013). N_e estimates are affected by transmission rates and therefore almost always cannot be scaled directly to the number of infected individuals (Frost & Volz, 2010). Furthermore, uneven sampling strategies such as focused sampling during transmission peaks can bias the estimation of effective population size (Karcher *et al.*, 2020; Parag *et al.*, 2020; Cappello & Palacios, 2022). Nevertheless, estimates of N_e can provide important information about the viral outbreak dynamics, including capturing seasonality or the possible efficacy of interventions in reducing subsequent outbreak size (Frost & Volz, 2010; Rife *et al.*, 2017; Drummond *et al.*, 2005) (Figure 2A).

Methods that are commonly employed to estimate population size trajectories over an epidemic include the **Bayesian skyline** (Drummond *et al.*, 2005), the **skyride** (Minin *et al.*, 2008), the **birth–death skyline** (Stadler *et al.*, 2013), and the **skygrid** (Gill *et al.*, 2013).

Several approaches estimate population size history alongside other tree parameters based on the principle that when the population size is small, sampled viruses are more likely to share a common ancestor in the very recent past, and therefore lineages coalesce (join) faster (Drummond *et al.*, 2005). Therefore, a faster rate of branch coalescence suggests a comparatively smaller population at that time point (Drummond *et al.*, 2005). The **Bayesian skyline model** requires pre-determination of the number of points at which effective population size can change, generating estimates that are summaries of multiple step-wise changes (Drummond *et al.*, 2005). The **skyride model** does not require predefined points, and introduces a method of temporal smoothing based on the assumption that N_e is correlated across successive coalescent intervals (Minin *et al.*, 2008). The **skygrid model** modifies and extends the skyride model by allowing the N_e trajectory to change at specific time-points pre-specified by the user (Gill *et al.*, 2013). A further extension of the skygrid model implements a generalized linear model (GLM) to test how time-varying covariates, such as monthly temperature, are associated with temporal changes in N_e in a method known as "**skygrid-GLM"** (Gill *et al.*, 2016).

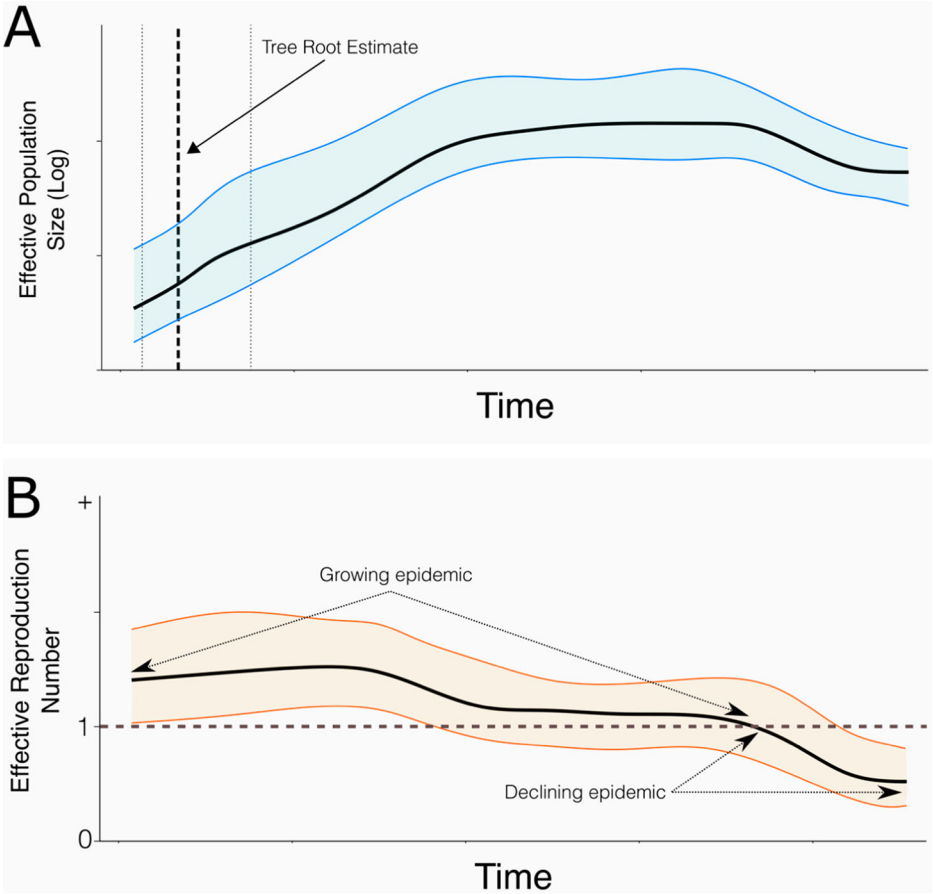

Figure 2. Exemplar outputs of phylodynamic methods used to infer past demographic parameters. A: Effective population size (N_e) over time: the solid line is the posterior median estimate for N_e, and the surrounding ribbon indicates the 95% Bayesian credibility interval. The bold vertical dashed line represents the median estimate of the time of the root. Thinner vertical lines indicate the lower (left) and highest (right) values of the 95% highest posterior density interval for the root age. B: Effective reproduction number (R_e) over time: the solid line is the posterior median estimate for R_e, and the surrounding ribbon indicates the 95% Bayesian highest posterior density interval. The horizontal dashed line indicates R_e of 1.

The **birth–death skyline** (Figure 2) provides an alternative method to these coalescent-based approaches (e.g. Bayesian skyline, skyride, and skygrid) (Stadler *et al.*, 2013). While in the Bayesian skyline approach only the effective population size changes over time, the birth–death skyline model infers temporal changes in transmission, death/recovery, and sampling rates at discrete intervals alongside variation in population size (Stadler *et al.*, 2013). Birth–death models infer a forward-in-time process, starting with the common ancestor of all sampled infections, followed by bifurcating new lineages representing observed and unobserved transmission events, thus generating a tree (Stadler *et al.*, 2013). In contrast, the coalescent is modelled backwards-in-time starting from the sampled sequences in the present time until the most recent common ancestor of the sample in the past, with the internal nodes representing the merging or coalescing of two lineages into their most recent common ancestor (i.e. coalescent event) (Drummond *et al.*, 2005; Frost & Volz, 2010).

Compared to coalescent approaches, birth–death skyline models can more easily explicitly infer the number of expected secondary infections caused by an infected individual (Figure 2B), either as a time-varying average ($\mathbf{R_e}$: **effective reproduction number**), or at the start of an outbreak when all individuals are considered as a completely susceptible population ($\mathbf{R_0}$: **basic reproduction number**) (Stadler *et al.*, 2012, 2013; Volz *et al.*, 2013). Changes in effective reproduction number can reflect depletion of the susceptible population as well as control interventions, with $R_e > 1$ indicating a growing epidemic, $R_e < 1$ a declining epidemic, and $R_e \approx 1$ that the outbreak is stable (Stadler *et al.*, 2013; Domingo, 2020; Gostic *et al.*, 2021).

Factors and settings associated with viral movement

To identify factors associated with higher rates of cross-species AIV transmission or lineage dispersal, phylodynamic analyses previously relied primarily on *post-hoc* literature searches for relevant events that occurred concurrently with reconstructed viral movements (Vijaykrishna *et al.*, 2013). For example, one study suggested that higher rainfall might increase H10 subtype AIV spillover from wild aquatic birds to poultry in Australia because inferred spill-over events occurred more frequently during periods of increased rainfall in the region (Vijaykrishna *et al.*, 2013). More recently, the incorporation of GLMs into discrete trait analyses (frequently referred to as "DTA-GLMs") (Box 1) (Lemey *et al.*, 2012, 2014; Gill *et al.*, 2016) has enabled hypotheses to be formally tested during the phylogenetic estimation process (Beard *et al.*, 2014). For instance, a DTA-GLM showed that H5N1 spill-over from wild birds to poultry in Egypt tended to occur in locations with a higher density of birds and humans, higher elevation, and several meteorological variables (Magee *et al.*, 2015).

To implement effective infection control, it is necessary to understand the settings in which AIVs move between wild and domestic birds. AIV outbreaks frequently occur in Asian wetlands or rice fields where free-grazing ducks are reared at high density and in close contact with wild birds, suggesting that these areas may support transmission between wild and domestic birds (Hulse-Post *et al.*, 2005; Martin *et al.*, 2011; Cappelle *et al.*, 2014; Prosser *et al.*, 2016; Sullivan *et al.*, 2018). Several phylodynamic analyses have supported this epidemiological finding, for example, indicating that the spread and maintenance of H5N8 lineages in the Republic of Korea were positively associated with regions of high wild waterfowl immigration and domestic duck density (Hill *et al.*, 2015). Low precision of metadata on sampled locations of virus sequences often limits analyses to considering predictors at district-level scales, making it harder to account for local heterogeneity in ecological suitability for wild birds or farming intensity (Hill *et al.*, 2015; Bahl *et al.*, 2016; Hill *et al.*, 2020). Furthermore, these methods have not been frequently applied in regions such as Africa and the Middle East where AIV genomic surveillance is limited (Naguib *et al.*, 2019; Ayala *et al.*, 2020; Kalonda *et al.*, 2020).

Between avian and mammalian species

HPAIVs and LPAIVs can occasionally infect humans and therefore are a public health threat (Webster *et al.*, 1992; Li *et al.*, 2019; Lycett *et al.*, 2019). Epidemiological studies suggest that most infected patients had recent exposure to live poultry or had visited live-bird markets, rather than exposure to wild birds or non-avian species (Zhou *et al.*, 2013; Yu *et al.*, 2014; Yang *et al.*, 2017; Li *et al.*, 2019; Oliver *et al.*, 2022). Phylogenetic analyses of virus genomes from humans and birds have been frequently used to support that poultry were the likely origin (Liu *et al.*, 2013; Joseph *et al.*, 2017; Yang *et al.*, 2017; Zhang *et al.*, 2021). Sporadic AIV transmission from birds to mammals can, in theory, select for variants that have increased transmissibility in mammals (Balzli *et al.*, 2016; Bourret, 2018; Nuñez & Ross, 2019; Zhao *et al.*, 2019) and therefore potentially increase pandemic risk (Nelson *et al.*, 2012; Bourret, 2018; Bravo-Vasquez *et al.*, 2020). Phylogenetic analyses have identified multiple AIV lineages associated with cross-species transmission from birds to swine or other mammals (Bodewes *et al.*, 2016; Ramey *et al.*, 2017; Zhao *et al.*, 2019; Chauhan & Gordon, 2021; Rijks *et al.*, 2021). These transmission events sometimes result in sustained transmission, particularly within swine populations (Nelson *et al.*, 2015; Bourret, 2018). For example, a phylodynamic study used time-calibrated phylogenies to determine that H10N7 viruses that caused significant mortality in harbour seals (*Phoca vitulina*) in 2014 in Europe were closely related to various avian-origin H10N7 viruses detected in wild birds in the Netherlands (Bodewes *et al.*, 2015, 2016). More recently, H5Nx clade 2.3.4.4b viruses in red foxes and wild birds in Europe (the Netherlands) were found to be closely genetically related (Rijks *et al.*, 2021). Our understanding of the frequency of spill-over to, and dissemination within, mammalian

species is limited by the sparseness of virus genomic surveillance in these taxa (Runstadler *et al.*, 2013; Bodewes *et al.*, 2016; Ren *et al.*, 2016).

Domestic poultry populations

HPAIV origins and diversification

HPAIVs pose a severe problem for the poultry industry, and understanding their origins could help predict and prevent future outbreaks (Nuñez & Ross, 2019; Beerens *et al.*, 2021). Time-calibrated phylogenies of HA show that multiple H5 and H7 HPAIV genotypes have independently evolved from ancestral LPAIV viruses, potentially facilitated by high poultry density and contact rates within intensive farming systems (Monne *et al.*, 2014; Dhingra *et al.*, 2018; Seekings *et al.*, 2018; Escalera-Zamudio *et al.*, 2020). Phylogeographic investigations have tracked the geographic origins of multiple HPAIV genotypes, and in rare cases, even suggested a possible source farm (Monne *et al.*, 2014; Dhingra *et al.*, 2018; Seekings *et al.*, 2018).

Geographic spread within poultry populations

Discrete trait analyses (Box 1) have frequently been employed to reconstruct AIV spatial spread within domestic poultry populations (Jin *et al.*, 2014; Bahl *et al.*, 2016; Zhang *et al.*, 2020; Harvey *et al.*, 2021). For example, southern China was shown to be an epicentre for the national spread of H5N6 HPAIV in poultry from 2013 to 2017 (Zhang *et al.*, 2020) and was identified as a potential source of a national wave of H9N2 infections in domestic birds (Jin *et al.*, 2014).

Some studies have employed structured coalescent models (Box 1) to reconstruct AIV spatial spread in domestic poultry (Yang *et al.*, 2019; Hicks *et al.*, 2020). Such analyses have shown that viral diffusion tended to occur within, rather than between, North American states during an H5N2 outbreak (Hicks *et al.*, 2020). However, as previously described, sampling bias or the presence of unsampled locations (Box 1) can be problematic for discrete trait phylogeographic models, and results must be interpreted with caution given regional differences in AIV genomic surveillance capacity (De Maio *et al.*, 2015; Layan *et al.*, 2023). LPAIV surveillance is particularly challenging because infections rarely cause severe disease in poultry and can easily be missed (Hurt *et al.*, 2014; Parvin *et al.*, 2020). Although HPAIV is likely easier to detect due to its higher pathogenicity, in some countries farmers may avoid reporting HPAIV cases for fear that birds will be culled without financial compensation (Chattopadhyay *et al.*, 2018; Parvin *et al.*, 2020; Moyen *et al.*, 2021; Ripa *et al.*, 2021).

Phylogeographic analysis can be performed using continuous models (Box 1) in which the spread of viruses is modelled using geographical coordinates (Lemey *et al.*, 2009, 2010). Continuous phylogeographic analyses can be preferable to discrete analyses when it is beneficial to understand virus spread in both sampled and intermediate unsampled locations (Box 1) (Lemey *et al.*, 2009, 2010). Continuous phylogeographic analysis indicated that the HPAIV H5N1 movement in Java in 2003 was characterized by short-range dispersal events interspersed with occasional long-range movements (Lam *et al.*, 2012). Similar approaches were also used to show that short-distance viral movement was more common than long-distance movements during Italy's 2016–17 HPAI H5N8 epidemic, with the first outbreak wave generally restricted to the north-eastern areas of the country (Harvey *et al.*, 2021). Biased sampling between geographical locations can result in a failure to determine the true origin of the outbreak and in the underestimation of viral diffusion rates into an oversampled region from an undersampled area when using continuous phylogeographic methods (Hill *et al.*, 2021; Kalkauskas *et al.*, 2021). The incorporation of sequence-free samples from affected yet unsampled areas may somewhat alleviate the effect of sampling bias in continuous phylogeographic analyses (as proposed in Kalkauskas *et al.* (2021)). However, this approach requires a prior understanding of the spatial distribution of outbreaks.

Drivers of dispersal

Understanding which species or breeds are most important for maintaining AIV within poultry systems can allow for the preferential targeting of surveillance and control efforts toward certain host types (Hill *et al.*, 2015; Barman *et al.*, 2017; Hicks *et al.*, 2020; Youk *et al.*, 2020; Harvey *et al.*, 2021). A study using Markov jump and reward analysis showed that, in live bird markets in the Republic of Korea, the transmission rate of H9N2 from domestic ducks to chickens was higher than the rate in the opposite direction (Youk *et al.*, 2020). Similarly, structured coalescent approaches (Box 1) demonstrated that the H5N2 viral transmission rates from layer chicken to turkey populations were higher than the reverse during a 2014–2015 outbreak in North America (Hicks *et al.*, 2020).

Phylogeographic analyses helped identify factors associated with AIV spread in domestic birds (Yang, Müller, *et al.*, 2019; Dellicour, Lemey, *et al.*, 2020; Dellicour, Lequime, *et al.*, 2020; Hicks *et al.*, 2020), thus highlighting which components of the production system may be most affected in future outbreaks. DTA-GLMs (Box 1) are commonly used for this purpose and have identified several economic and agricultural factors significantly associated with AIV dispersal in

domestic birds in China (such as poultry population density, freight transportation, the number of markets selling poultry or poultry products, and high human density) (Lu *et al.*, 2017). When both precise location and detailed geographical environmental data are available, we can also investigate factors associated with viral dispersal in a continuous phylogeographic analysis using the R package "*seraphim*" (Dellicour *et al.*, 2016) (Box 1). For example, this approach identified weak support for the association of several spatial factors (e.g. human, chicken and duck population densities, inaccessibility, savanna) with heterogeneity in lineage dispersal velocity of H5N1 in the Mekong region (Cambodia, Laos, Thailand, Vietnam) (Dellicour, Lemey, *et al.*, 2020).

The impact of commercial poultry movement networks on AIV dissemination in domestic birds represents an important, but particularly challenging, area of research (Lu *et al.*, 2017; Yang *et al.*, 2020; Moyen *et al.*, 2021). Poultry trading records are difficult to obtain on a large scale, especially in low- and middle-income countries where poultry production systems can be highly complex and dynamic, and where these data are not already routinely collected (Yang *et al.*, 2020; Moyen *et al.*, 2021). As such, most phylogeographic studies have used proxies for poultry trade networks (Lu *et al.*, 2017; Yang *et al.*, 2020). For example, one study used DTA-GLMs (Box 1) to show that a proxy network of poultry transportation in China, as determined by a gravity model built from metrics of domestic poultry production and egg production, was positively associated with the large-scale movement of three AIV subtypes (H5N1, H7N9, and H5N6) (Yang *et al.*, 2020). Greater availability of accurate poultry trade data would likely allow for more rigorous assessment of the impact of poultry movements on AIV dispersal (Parvin *et al.*, 2020; Yang *et al.*, 2020; Moyen *et al.*, 2021).

Across borders

Although AIV dispersal in domestic poultry typically occurs within countries, several phylodynamic studies have investigated lineage movements across borders (Melville & Shortridge, 2006; Yang, Müller *et al.*, 2019; Yang, Xie *et al.*, 2019). The occurrence of long-distance trade-facilitated AIV movements was highlighted by a 2004 report that linked the 1500 km spread of HPAIV H5N1 from Lanzhou (Gansu Province, Northwest China) to Lhasa (Tibetan Autonomous Region) to the transport of domestic birds (Melville & Shortridge, 2006). More recently, studies have begun to explore larger-scale factors that can drive interprovincial or international virus movement (Yang, Müller *et al.*, 2019; Yang, Xie, *et al.*, 2019). Through a GLM extension of a structured coalescent model (Box 1), one study identified annual levels of international live poultry trade between countries and national poultry production as predictors of cross-border H9N2 virus movement in domestic Asian birds (Yang, Chowdury *et al.*, 2019). Illegal trade may also drive the international spread of AIV. However, phylodynamic investigations are limited in their ability to investigate the impact of illegal bird trade on the global dispersal of AIV, as this predictor cannot be easily quantified (Tian, Zhou, *et al.*, 2015; Yang, Müller, *et al.*, 2019; Yang, Xie, *et al.*, 2019).

5.5. Evaluating control efforts

In addition to helping guide the design of novel measures aimed at tackling AIV spread, phylodynamic analyses have been used to evaluate the efficacy of previously implemented control measures (Lee *et al.*, 2014; Tian, Cui, *et al.*, 2015; Nickbakhsh *et al.*, 2016; Kwon *et al.*, 2020; Chakraborty *et al.*, 2022). By incorporating time-varying predictors into a GLM extension of a structured coalescent phylogeographic model (Box 1), one study showed that duck culling in France likely reduced the spread of HPAIV H5N8 between French administrative divisions (Chakraborty *et al.*, 2022). Several studies have also employed phylodynamic methods that infer past population demographic dynamics to explore the effectiveness of control measures (Lee *et al.*, 2014; Tian, Cui, *et al.*, 2015; Kwon *et al.*, 2020). For example, Kwon *et al.* (2020) argued that an observed fall in H5N1 virus effective population size in Bangladesh over 3 years was due to reduced virus prevalence in domestic birds following the concurrent introduction of wide-scale vaccination, although alternative explanations are possible (Kwon *et al.*, 2020). Likewise, one study used estimates of effective reproduction numbers (Box 2) to infer that HPAI-targeted control measures (e.g. culling of infected flocks, pre-emptive culling of neighbouring flocks) introduced in Italy in 2000 successfully slowed the epidemic growth of a novel HPAI outbreak but not that of its LPAI progenitor lineage (Nickbakhsh *et al.*, 2016).

Outlook

Whilst this review highlights where phylodynamic analyses have contributed significantly to our understanding of AIV over the last few decades, we identify several areas that can aid future progress of the field. First, we can benefit from the wide range of new approaches developed and extended during the COVID-19 pandemic. For example, methods that enable accessible, "real-time" and easily scalable incorporation of sequences into viral phylogenies (e.g. Nextstrain (Hadfield *et al.*, 2018)) could be used more extensively to support surveillance, and methods that incorporate host travel history within

phylogeographic analyses could be explored to accommodate bird migration histories (Lemey *et al.*, 2020).

Despite many recent methodological advances, formally integrating different data types within phylodynamic analyses remains a key challenge (Frost *et al.*, 2015; Baele *et al.*, 2017). Approaches that can better integrate temporally varying environmental and demographic data alongside genetic sequences would be extremely valuable to study how bird movements drive AIV lineage spread. Ideally, such models would be developed to handle a broad array of new data types, including bird tracking data from mobile global positioning systems (e.g. GPS-3G-Bluetooth technologies developed to investigate bird spatial behaviour (Yu *et al.*, 2022)), satellite imagery of high-risk locations for AIV transmission between wild and domestic species, and poultry trade data. In locations where it is difficult for authorities to access trading records comprehensively, purpose-built apps could facilitate collection of more complete poultry trade network data for use in such new models (Ravindran, 2021; Grubaugh *et al.*, 2019; Lycett *et al.*, 2019; Cardona-Ospina *et al.*, 2021). The development of methods that effectively accommodate reassortment in phylodynamic analyses in a user-friendly fashion would help better understand AIV spread (Frost *et al.*, 2015; Lycett *et al.*, 2019; Verhagen, Fouchier, *et al.*, 2021).

It is essential to improve AIV genome sequence and metadata availability (Kalkauskas *et al.*, 2021; Layan *et al.*, 2023). Missing metadata (such as date of collection, host type or species, precise location for wild birds, or production context for domestic poultry) reduces the value of virus genomes within phylodynamics. Likewise, as discussed throughout this review, sampling biases increase the risk of drawing incorrect conclusions from phylodynamic analyses. It is therefore important to grow capacity for AIV genomic monitoring in currently under-represented countries and sampling from understudied species.

Finally, tackling challenges related to feasibility and resource-intensity is essential for enhancing phylodynamic studies of AIVs. At present, and particularly when dealing with large genomic datasets, a significant level of technical expertise and robust computing infrastructure is often required to formulate appropriate phylodynamic models, execute them, and interpret their results (Duchene *et al.*, 2018; Sagulenko *et al.*, 2018; Attwood *et al.*, 2022). As such, the continued development of faster tools (e.g. recently introduced ML methods (Sagulenko *et al.*, 2018; Ishikawa *et al.*, 2019)) and the advancement of computational packages that allow existing tools to make more effective use of available computer hardware (e.g. BEAGLE (Ayres *et al.*, 2012)) are critical, especially in more resource-constrained environments and where results are intended to inform emergency responses (Suchard & Rambaut, 2009; Baele *et al.*, 2019). The use of cloud computing in phylodynamic analyses, which was critical for handling the unprecedently large genomic datasets produced the COVID-19 pandemic, could be beneficial in helping researchers handle increased numbers of genome sequences. Greater investment in appropriate training and computational infrastructure in many lower- and middle-income countries would improve global accessibility of phylodynamic approaches (Rife *et al.*, 2017; Hill *et al.*, 2021; Attwood *et al.*, 2022).

Conclusions

AIVs can severely harm domestic and wild birds, and their effective control in birds can help protect the health of humans and other mammalian species. Phylodynamic approaches can be insightful in reconstructing the spatiotemporal dispersal of AIVs, with models capable of analysing viral diffusion within and between different host populations and locations. However, limitations in phylodynamic models exist when key metadata are missing, virus genomic sampling is uneven, and for analysing reassortant viruses. Addressing these challenges will be important to further fulfil the potential of phylodynamic analyses to improve human and animal health.

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Additional Information

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