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LETTER

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Functional traits explain waterbirds' host status, subtype richness, and community-level infection risk for avian influenza

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Abstract

Species functional traits can influence pathogen transmission processes, and consequently affect species' host status, pathogen diversity, and community-level infection risk. We here investigated, for 143 European waterbird species, effects of functional traits on host status and pathogen diversity (subtype richness) for avian influenza virus at species level. We then explored the association between functional diversity and HPAI H5Nx occurrence at the community level for 2016/17 and 2021/22 epidemics in Europe. We found that both host status and subtype richness were shaped by several traits, such as diet guild and dispersal ability, and that the community-weighted means of these traits were also correlated with community-level risk of H5Nx occurrence. Moreover, functional divergence was negatively associated with H5Nx occurrence, indicating that functional diversity can reduce infection risk. Our findings highlight the value of integrating trait-based ecology into the framework of diversity–disease relationship, and provide new insights for HPAI prediction and prevention.

KEYWORDS
dilution effect, diversity–disease relationship, functional divergence, functional diversity, HPAI H5Nx, pathogen diversity

INTRODUCTION

Community composition can affect the transmission dynamics of multi-host pathogens and downstream infection risk (Keesing et al., 2006). Many studies have suggested that species diversity within communities, as one of the most important attributes of community composition, can be correlated with disease risk (i.e., the diversity–disease relationship) through a variety of mechanisms (Huang et al., 2017; Johnson et al., 2015;

Shenglai Yin and Ning Li contributed equally to this work.

Keesing & Ostfeld, 2021; Ostfeld & Keesing, 2012). However, the direction and strength of this relationship are still debated (Halliday et al., 2020; Huang et al., 2016; Liu et al., 2020; Magnusson et al., 2020; Rohr et al., 2020). Particularly, the majority of studies have focused on community taxonomic diversity (e.g., species richness) or phylogenetic diversity, while more rarely do studies consider the effects of community functional diversity. Considering ongoing anthropogenic activities (e.g., deforestation, climate change) and their strong influences on community functional diversity (Etard et al., 2022), understanding the effects of functional diversity on infection risk is imperative for the prediction and prevention of pathogen transmission.

The effects of community functional diversity on infection risk can result from the influence of species' functional traits on their fundamental epidemiological characteristics. These characteristics, including but not limited to host exposure (i.e., contact), susceptibility (i.e., the probability of infection given contact), and suitability (i.e., pathogen development within the host), govern the ability of hosts to transmit pathogens to new hosts (Becker, Seifert, & Carlson, 2020; Downs et al., 2019; Merrill & Johnson, 2020). Diverse hypotheses have been proposed to explain species-level correlations between functional traits and these epidemiological characteristics. For example, species that differ in foraging ecology (e.g., trophic level, foraging strata) and behaviour (e.g., migration strategy, sociality) may vary in their exposure to pathogens (Smith et al., 2021). In addition, life history theory suggests trade-offs between investment in reproduction and immune defences, such that fast-lived species (i.e., small-bodied hosts with high fecundity and short lifespans) may have higher pathogen susceptibility and suitability (Albery & Becker, 2021; Huang et al., 2013; Valenzuela-Sánchez et al., 2021).

Given the role of species' exposure, susceptibility, and suitability in governing infection outcomes, functional traits that affect these epidemiological characteristics can determine both host status (i.e., whether a species can be infected by a specific pathogen) and pathogen diversity (i.e., the diversity of pathogens that infect a host species). Such relationships between functional traits and these two species-level infection outcomes have been observed across a diverse range of study systems (Albery & Becker, 2021; Stephens et al., 2016). For example, diet was found to be associated with host status for both the Ross River virus (Walsh, 2019) and the rabies virus (Worsley-Tonks et al., 2020). Similarly, pathogen richness (i.e. the number of pathogen species) was positively correlated with mammalian body mass and longevity (Huang et al., 2015) as well as seasonal migration in ungulates (Teitelbaum et al., 2018). Although many studies have explored factors associated with these species-level infection outcomes, important gaps remain. Particularly, previous studies of pathogen diversity have mainly focused on taxonomic richness of pathogens, while few have asked comparative questions regarding the diversity (e.g., genetic or antigenic) within a pathogen species (Becker, Speer, et al., 2020; Fountain-Jones et al., 2017). Because many pathogen lineages can show cryptic host specificity (Streicker et al., 2010; Withenshaw et al., 2016), defining pathogen diversity at the within-species level and identifying the predictors of this variation could generate more realistic insights and predictions about pathogen transmission in complex host communities.

Given the effects of functional traits on epidemiological characteristics and infection outcomes at the species level, functional diversity, defined as the distribution (i.e. the value, range, and relative abundance) of the functional traits measured in a given community (Garnier et al., 2016), may also influence infection risk at the community level. However, this hypothesis has rarely been tested. A recent study found that the severity of foliar disease in Alpine meadows was associated with the community weighted mean (CWM, representing the mean value of a trait in the community) of life-history traits (Halliday et al., 2021). However, the relative contribution of life-history traits to other functional traits (e.g., foraging or behavioural traits) in the context of functional diversity has not been assessed, and the importance of other metrics of functional diversity (e.g., metrics representing functional divergence) remains unknown. Greater investigation into the effects of community functional diversity on infection is needed to complete our understanding of the diversity–disease relationship.

Avian influenza virus (AIV), particularly highly pathogenic avian influenza (HPAI) virus, has caused substantial public concerns due to its frequent occurrence and high mortality rates (Verhagen et al., 2021). Many wild birds, particularly waterbirds (i.e., waterfowl and shorebirds), serve as the natural reservoir hosts for AIV (Verhagen et al., 2021). However, waterbird species can display considerable variations in their exposure and susceptibility to AIV (Olsen et al., 2006; van Dijk et al., 2018). These variations have been proposed to stem from waterbird species' functional traits (Hill et al., 2010; van Dijk et al., 2018) or phylogenetic relationships (Gaidet et al., 2012; Wille et al., 2023), but these hypotheses have not been systemically tested. In addition, a few studies have suggested that waterbird community composition can influence AIV transmission risk (Gaidet et al., 2012). For example, a recent study showed that the phylogenetic diversity of waterbird communities was negatively associated with HPAI H5N1 outbreak risk in Europe (Huang et al., 2019). This study also proposed an untested hypothesis that the negative effect of community phylogenetic diversity might be attributed to the aggregations of closely related species (with similar behavioural and physiological traits) at shared habitats (Huang et al., 2019). Considering the ongoing wetland degradations worldwide and its strong effects on waterbird community composition, especially functional diversity (Green & Elmberg, 2014), it is imperative to understand the effects of waterbird functional traits on AIV transmission at both the species and community levels, particularly in the context of recently increasing HPAI outbreaks.

In this study, we first investigate the effects of waterbird functional traits (including foraging, behavioural, and life-history traits) on AIV host status and diversity (measured as subtype richness) at the species level. We then test whether community functional diversity (including CWMs and functional divergence) is associated with HPAI H5 (clade 2.3.4.4b) occurrence in European wild birds. We here focus on two epidemics, the 2016/17 epidemic and 2021/22 epidemic, which were respectively dominated by the H5N8 and H5N1 subtypes. We predict that fast-living waterbird species (i.e., with smaller body mass, higher clutch size, shorter longevity) are more likely to host AIV and have higher AIV subtype richness, as they may have higher susceptibilities due to lower investment in immune defences. A higher probability of AIV hosting and greater subtype richness may also be correlated with those traits that can facilitate exposure to the virus (e.g., migration, gregariousness, and high dispersal ability). In addition, owing to the positive correlations predicted with these species-level infection outcomes, communities with higher CWMs of these same traits would be expected to have a higher probability of HPAI H5Nx occurrence. In contrast, we predict that functional divergence could be negatively associated with H5Nx occurrence, as the aggregations of closely related species at shared habitats should promote virus spread within host communities.

MATERIALS AND METHODS

Data on waterbird species' host status and subtype richness

We obtained information of sequenced AIV isolated from 1905 to 2021 from the Influenza Virus Resource at the National Center for Biotechnology Information (NCBI). These data include the AIV subtype and the host species from which the sequence was isolated. We here focused on only European waterbird species, for which a list of species was generated based on data collected from the International Waterbird Census program from Wetlands International (see below). Among the 143 European waterbird species included in this analysis, each was treated as a host species if AIV was isolated from that species. We also counted the total number of AIV subtypes historically isolated from each species (i.e., reported subtype richness). The AIV subtype here was defined based on hemagglutinin (HA) and neuraminidase (NA). Records without complete HA and NA information (i.e., only noted with Hx or Ny rather than complete HxNy) were counted as an independent subtype only when there was no other same Hx or Ny recorded. Since previous studies suggested that the non-parametric Chao2 estimator can represent pathogen diversity with high accuracy by lowering reporting bias (Teitelbaum et al., 2020), we also estimated the Chao2 index for each host species by treating each report as an independent sampling event (Huang et al., 2015; Teitelbaum et al., 2020). We list all waterbird species and their corresponding host status, reported subtype richness, and Chao2 index (Table S1).

Data of HPAI H5Nx occurrence and waterbird community in Europe

To investigate the effects of community functional diversity on HPAI H5Nx occurrence in Europe, we collected data of HPAI H5Nx (mainly H5N8) outbreaks in wild birds (together with their coordinates) during the 2016/17 epidemic (from August 2016 to July 2017) from the Food and Agriculture Organization of the United Nations (FAO). Data on waterbird communities across ~7000 sites in Europe during 2015–2017 were collected from the International Waterbird Census (IWC) program (http://iwc.wetlands.org) coordinated by Wetlands International. This dataset, containing waterbird species and their abundance (the total number of birds counted), was based on surveillance during the wintering season (mainly in mid-January; (Amano et al., 2018). Following previous studies (Julliard et al., 2006; Li et al., 2019), we kept the maximum number counted for each species among the years for sites with more than one year of data. In addition, to match the time of the waterbird surveys, we only analysed outbreaks between November and March, when the outbreak cases accounted for 97.1% of all cases in the epidemic. Since autumn of 2021, the HPAI H5 outbreaks were dominated by the H5N1 subtype (European Food Safety Authority et al., 2022), we therefore also analysed the H5Nx outbreaks during the 2021/22 epidemic to test whether the effects of community functional diversity indices were different between the two epidemics.

We then applied a cross-selection process to match the H5Nx outbreak sites and the waterbird census sites for each epidemic. Briefly, the waterbird data of a bird census site was assigned to a H5Nx outbreak site as a presence when the two sites were close enough (i.e., within 10 km, the HPAI surveillance zone radius applied in European Union countries (Pittman & Laddomada, 2008) and located in a similar habitat (e.g., grassland or crop field) around the same lake or river. A bird census site was assigned as an absence when this site was sufficiently far away (i.e., >60 km, three times the diameter for HPAI surveillance zones) from any H5Nx outbreak site. We also set a maximum distance (200 km) to the nearest outbreak site in the selection of absence locations, in order to limit the effect of false absences

(Dhingra et al., 2016). We only included absence sites in countries where H5Nx outbreaks occurred, and, as in prior studies (Si et al., 2010, 2013), in the maximum geographic range of H5Nx outbreaks (Figure S1). Following this processing, the final analysed dataset included 231 presences and 1714 absences for the 2016/17 epidemic, as well as 353 presences and 1636 absences for the 2021/212 epidemic.

Functional traits and diversity

We compiled functional traits across our waterbird species that were hypothesized to be associated with epidemiological characteristics underlying pathogen transmission. We collected five life-history traits (i.e., average body mass, incubation time, clutch size, longevity, and age of sexual maturity) and diet guild. Diet guild was derived from the EltonTraits database (Wilman et al., 2014), and defined from utilization ratios into three types of food resources: plants or seeds, invertebrates, and vertebrates (including carrion). We categorized diet guild as one of these three types if the utilization ratio of that type exceeded 50%; species were defined as omnivorous if the utilization ratios of each food group were all less than 50%. We also collected several behaviour traits, including migration strategy (i.e., sedentary, partially migratory or fully migratory), sociality (i.e. gregarious or solitary), and dispersal ability; the latter was measured via the avian hand-wing index (HWI), following previous studies (Smith et al., 2021). Because some traits (i.e., longevity and age of sexual maturity) contained missing values, we first searched for missing values in the published literature. If no results were found, we used nonparametric imputation algorithm *missForest* (Stekhoven & Stekhoven, 2013) to impute the missing values, as this algorithm has a low error rate (Fountain-Jones et al., 2019; Penone et al., 2014). All functional traits were collected from published datasets or primary literature (see Data Availability).

We next calculated a series of variables representing waterbird community functional diversity (FD variables) to test their effects on HPAI H5Nx occurrence at the community level. We first calculated, for each sampling site (i.e., presence or absence), the community weighted mean (CWM) for each functional trait. For each categorical (i.e., diet guild and migration strategy) or binary trait (i.e., sociality), the CWM provides the proportion of birds with that specific trait in the community. In addition to CWMs, we also calculated several functional divergence metrics. We first generated three dendrograms for diet guild, foraging strata, and behaviour traits (as a whole). Foraging strata contained the utilization ratios of three types of habitats: foraging around the water surface, foraging below the water surface, and ground foraging. We then calculated the standardized abundance-weighted mean pairwise distance (MPD) and standardized abundance-weighted mean nearest taxon distance (MNTD) based on these dendrograms. These two standardized metrics were calculated by implementing a null model that was generated by shuffling dendrogram tip labels 1000 times (Swenson, 2014). Following previous analyses (Dhingra et al., 2016), we also calculated mean human population density within a 5-km buffer zone to control for reporting bias. The human population densities in 2015 and 2020 were respectively used for the analyses of the 2016/17 and 2021/22 epidemic.

Statistical analysis

For both AIV host status and subtype richness, we first quantified phylogenetic signal, which here measures whether more phylogenetically similar species share similar infection outcomes (Revell et al., 2008). A high phylogenetic signal could be expected, given that the morphological, behavioural, and physiological traits of species that regulate pathogen exposure, susceptibility, and suitability are usually phylogenetically conserved (Olival et al., 2017; Wang et al., 2019, 2023; Wille et al., 2023). We constructed a consensus supertree from BirdTree by summarizing 2000 phylogenetic trees with the Hackett backbone for our 143 European waterbird species (Jetz et al., 2012). Phylogenetic signal in host status and subtype richness were respectively tested using the *D* value (Fritz & Purvis, 2010) and Pagel's λ (Freckleton et al., 2002). A *D* value approaching 0 suggests the binary trait has evolved according to Brownian motion (i.e., phylogenetic dependence), while a *D* value of 1 suggests the trait is randomly distributed across the phylogeny. In contrast, a λ value of 0 indicates no phylogenetic signal for a continuous trait, with λ of 1 suggesting phylogenetic dependence. Phylogenetic signal tests were implemented using the package '*caper*' (Orme et al., 2012) in R 4.2.0.

We then applied phylogenetic generalized linear models (PGLMs, logit link) and phylogenetic generalized least squares (PGLS) models, respectively, to test the effects of waterbird species' functional traits on their AIV host status and subtype richness. We here used the Chao2 index (log-transformed) as the measure of subtype richness in the main text, but also analysed the original number of reported subtypes (log-transformed) as supplementary results. Prior to analyses, we log-transformed body mass to reduce skewness. We compared candidate models for each dependent variable following a full-as-possible model-building strategy, removing aliased or collinear predictors (i.e., Spearman correlations >0.65, variance inflation factors, VIF, above 5) from any one model and limiting the number of predictors to allow at least 10 observations per estimated coefficient. We thus compared 10 models for host status and 9 models for subtype richness using Akaike information criterion (AIC) and derived Akaike weights (Anderson & Burnham, 2004).

In cases where multiple models fell within two ΔAIC, we followed principles of parsimony or performed model averaging of coefficients using the '*MuMIn*' package (Barton & Barton, 2015). Phylogenetic models were fitted in R 4.2.0 with the '*phylolm*' package (Tung Ho & Ané, 2014).

For both the 2016/17 and 2021/22 epidemics, we used generalized linear models (GLMs, logit link) to analyse the relationships between predictors and HPAI H5Nx occurrence at the community level. To reduce the number of potential candidate models, we only selected one of the aliased variables (i.e., CWMs of diet and migration strategy) to construct the full functional diversity model. We here kept the CWM of pland seed diet and fully migration as they had the smallest p-values in single-variable models. Based on the full functional diversity model, we then compared 16 candidate models for both epidemics, again following a full-as-possible model-building strategy. We reported both the values of the area under the Receiver Operating Characteristic (ROC) curve (AUC) and the Nagelkerke pseudo R^2 to measure model performance. In all GLMs, the mean human population density was retained to control for reporting bias.

We also determined the relative importance of community functional diversity indices in explaining the spatial pattern of HPAI H5Nx occurrence in wild birds. We thus collected other variables on waterbird community, as well as agro-climatic predictors that have previously been identified as risk factors for H5Nx (Dhingra et al., 2016). Other waterbird community variables included waterbird species richness, the total waterbird abundance within the community, and the abundances of high-risk species (Table S1), as classified by combining lists from previous studies (Schreuder, 2021; Veen et al., 2007). In addition, we also included the abundance of several specific species: Mallards (*Anas platyrhynchos*), Eurasian wigeon (*A. penelope*), and Tufted duck (*Aythya fuligula*), as these species were among the most identified species infected with H5Nx in 2016/17 epidemic (Alarcon et al., 2018). Agro-climatic variables were calculated, for each presence and absence, as the mean values within a 5-km buffer zone, and included the total length of the waterbody, mean chicken density in 2015, mean (domestic) duck density in 2015, mean temperature in the winter (December to February) of the corresponding year, and the precipitation in winter. With these variables, we then constructed two additional models, an agro-climatic partial model (i.e., only include all agro-climatic variables) and a community partial model (i.e., include all other waterbird community variables except for variables related to functional diversity). Again, in all multivariable models for H5Nx occurrence, the mean human population density was retained to control for sampling bias. With these two partial models and the full functional diversity model, we then conducted variation partitioning analysis based on the Nagelkerke pseudo R^2 to assess the relative contributions of functional diversity variables versus agro-climatic variables and other community variables to explain the spatial pattern of HPAI H5Nx occurrence. All H5Nx models were fitted in R 4.2.0.

RESULTS

AIV host status and subtype richness

Among the 143 European waterbird species, 82 species (57.3%) were recognized as AIV hosts, and the reported subtype richness was up to 100 for Mallard (Figure 1a). Anseriformes had the highest proportion of AIV host species (91.7%, $n=48$), followed by Podicipediformes (80%, $n=5$), Ciconiiformes (50%, $n=2$), and Charadriiformes (49.1%, $n=55$); Gaviiformes, Phoenicopteriformes, and Procellariiformes had no AIV host species (Figure 1b). The Anseriformes also had the highest mean AIV subtype richness (10.62±2.49), followed by Charadriiformes (3.89±1.65; Figure 1b). Both host status ($D=0.517$) and subtype richness ($\lambda=0.558$) showed moderate phylogenetic signal.

We performed phylogenetic comparative analyses to test the effects of waterbirds' traits on both host status and subtype richness. For host status, only the top model was competitive ($w_i=0.99$, all other models had ΔAIC >16; Table S2). The results of this top model (Table 1) suggested that body mass and hand-wing index (HWI) were positively correlated with host status (Figure 2a,b), while the age of sexual maturity showed a negative correlation with host status (Figure 2c). In addition, waterbird species with an invertebrate diet tends to have a higher probability of being an AIV host (Table 1).

For AIV subtype richness (i.e., Chao2 index), only two models were competitive ($w_i=0.52$ and 0.36, all other models had ΔAIC >5; Table S3). Model averaging (Table 1) revealed that subtype richness was positively correlated with species' clutch size (Figure 2d), HWI (Figure 2e), and longevity (Figure 2f), while species with a vertebrate diet had lower subtype richness (Table 1). In addition, the analyses of the original reported number of AIV subtypes generated similar results as the analyses of the Chao2 index (Table S4).

Effects of community functional diversity on HPAI H5Nx occurrence

We fit GLMs to investigate the effects of community functional diversity on HPAI H5Nx occurrence in Europe in both the 2016/17 and 2021/22 epidemics. We found that only the top model was competitive for 2016/17 epidemic ($w_i=0.73$, all other models had ΔAIC >2; Table S5), while three models were competitive for 2021/22 epidemics ($w_i=0.38$, 0.21, and 0.20, all other

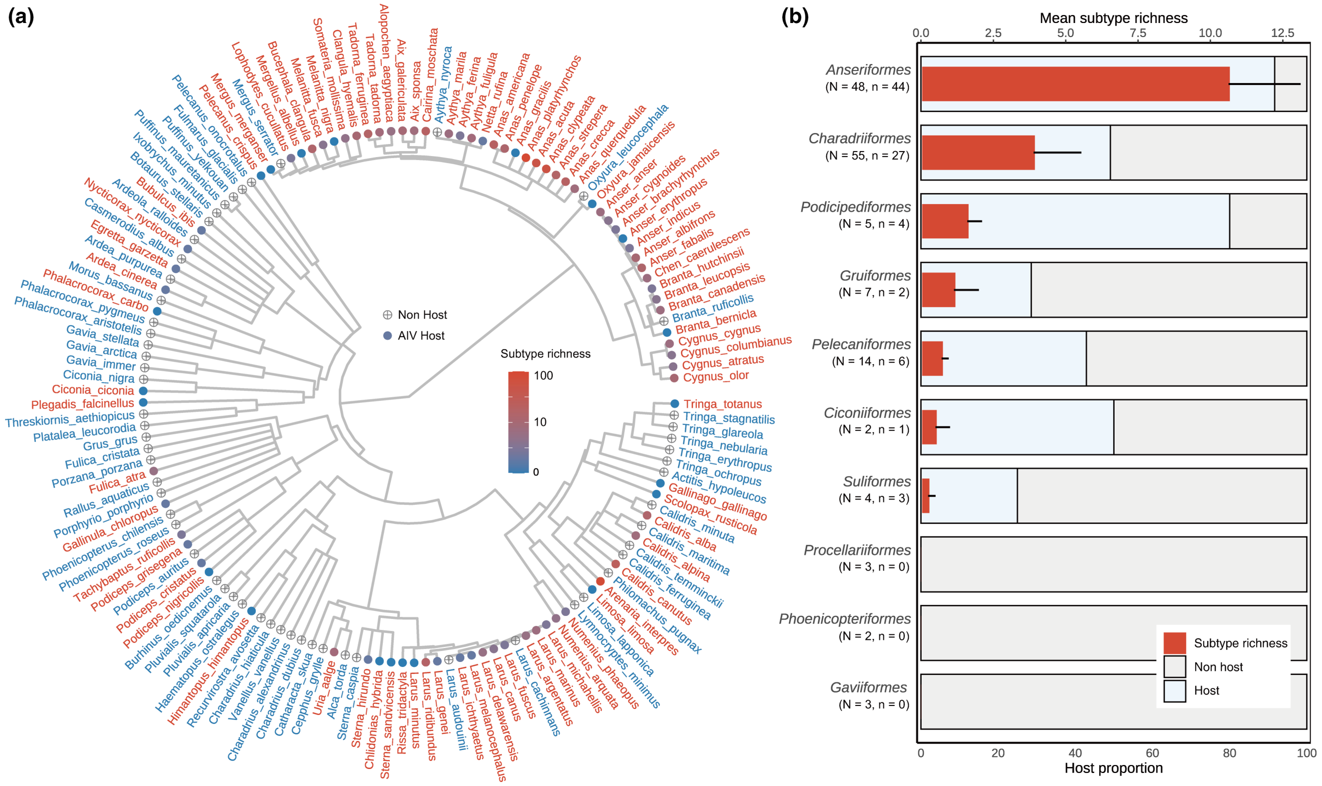

FIGURE 1 The phylogeny (a) and descriptive results (b) of AIV host status and reported subtype richness. The error bars in (b) indicate the standard error of mean reported subtype richness, *N* and *n* are respectively the total number of species and the number of host species for each order.

TABLE 1 The estimated regression coefficients (b±SE) and corresponding *z*-values of the comparative regression models for AIV host status and subtype richness.

	Host status			**Subtype richness, log(Chao 2)**		
Trait predictors	***b***	***z***	***p*-value**	***b***	***z***	
Body mass	0.64±0.25	2.53	0.011*	−0.07±0.16	−0.46	0.65
Clutch size	0.009±0.10	0.086	0.93	0.47±0.16	2.98	0.003**
Incubation time	−0.018±0.04	−0.42	0.67	0.19±0.15	1.28	0.20
Longevity	0.025±0.019	1.34	0.18	0.49±0.45	3.34	<0.001***
Age of sexual maturity	−0.67±0.23	−2.97	0.003**	−0.09±0.18	−0.49	0.63
Hard-wing index (HWI)	0.072±0.03	2.37	0.018*	0.35±0.13	2.64	0.008**
Gragarious	0.31±0.41	0.75	0.45	−0.14±0.33	−0.44	0.66
Invertebrate diet	1.41±0.49	2.88	0.004**	—	—	—
Vertebrate diet	—	—	—	−0.71±0.32	−2.19	0.028*
Partial migration	—	—	—	0.23±0.27	0.86	0.39
Full migration	−0.69±0.38	−1.81	0.07	−0.08±0.26	−0.33	0.74

*$p<0.05$; **$p<0.01$; ***$p<0.001$.

models had ΔAIC >2; Table S6). Both the community-weighted means (CWMs) and the functional divergence indices were significantly associated with H5Nx occurrence (Figure 3). For both epidemics, the probability of H5Nx occurrence was positively correlated with the CWMs of clutch size and plant seed diet, and negatively associated with the proportion of solitary birds (Figure 3). In addition, H5Nx occurrence in the 2016/17 epidemic was also positively associated with the CWMs of body mass, and hand-wing index (HWI); and occurrence was negatively associated with the proportion of birds with full migration, as well as the MPD of forage strata and MNTD of diet. In the 2021/22 epidemic, H5Nx occurrence was also positively correlated with the CWM of longevity and the proportion of fully migratory birds, and negatively correlated with the CWM

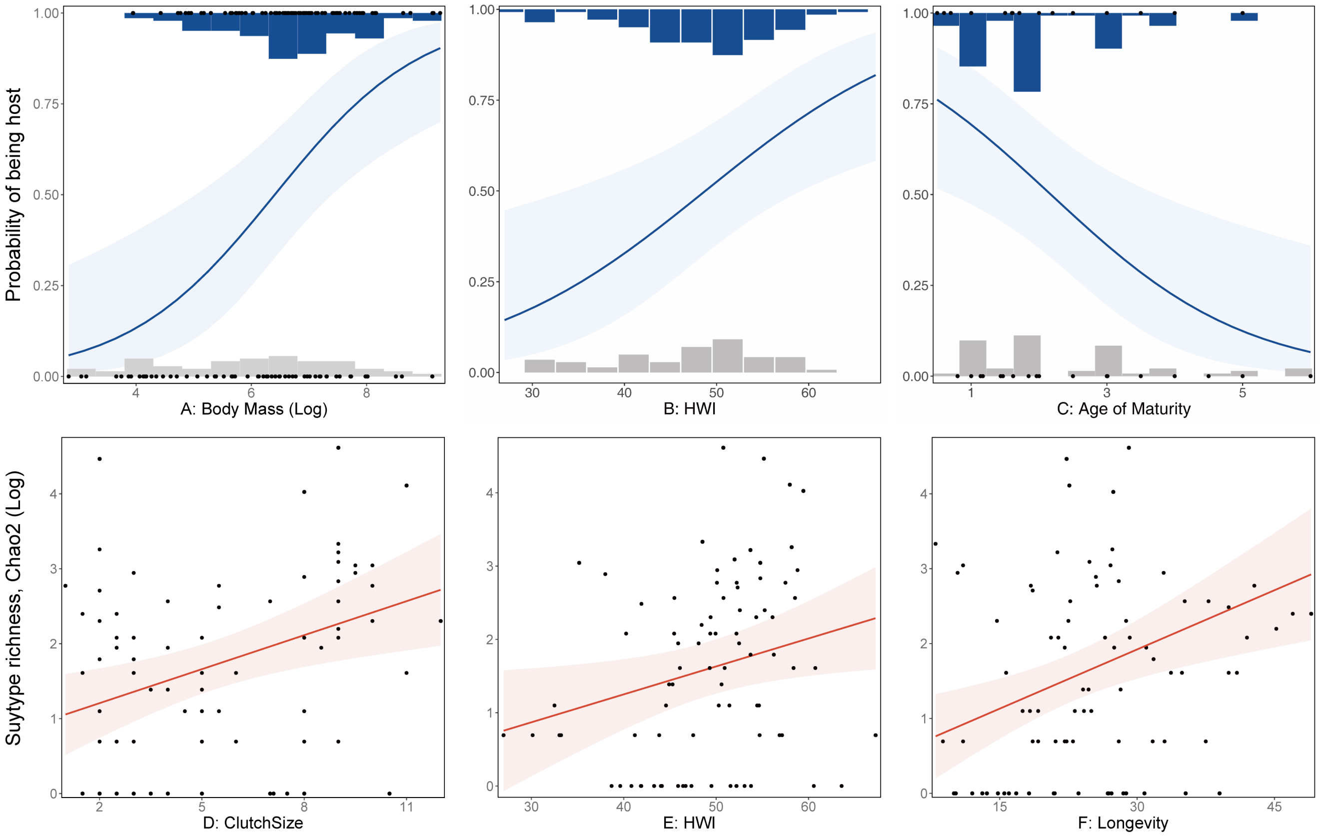

FIGURE 2 Partial effects of functional traits on species-level infection outcomes (blue lines: host status; red lines: Chao 2 subtype richness).

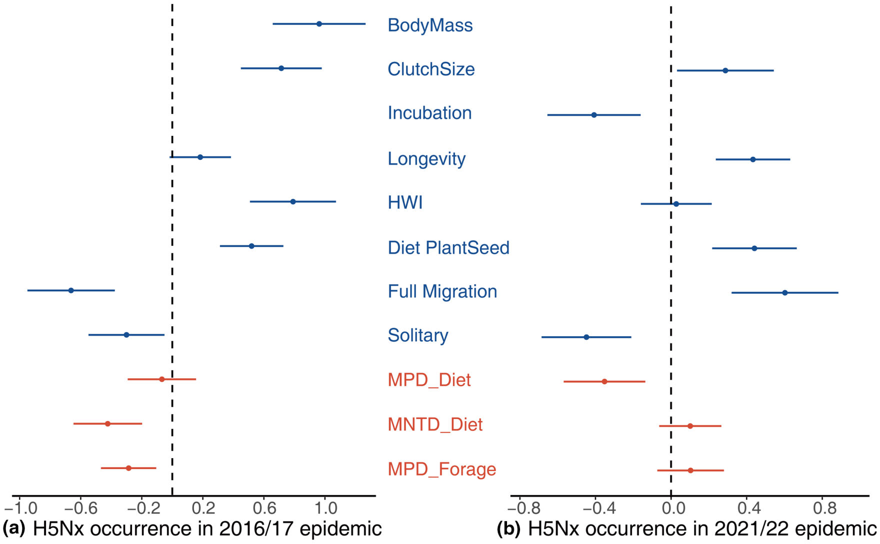

FIGURE 3 The regression coefficients (and 95% CI) for the functional diversity models of HPAI H5Nx occurrence in the 2016/17 (a) and 2021/22 (b) epidemics. Blue, community-weighted mean variables; Red, functional divergence variables.

of incubation as well as the MPD of diet (Figure 3). The top models could explain respectively 31.9% and 48.9% of the variation in HPAI H5Nx occurrence in the 2016/17 and 2021/22 epidemics, and performed well (AUC = 0.844 and 0.871).

Variation partitioning analyses (Figure 4) showed that functional diversity variables explained a relatively smaller proportion of H5Nx variation (4.3%) compared to the agro-climatic variables (9.4%) or other community composition variables (7.7%) in the 2016/17 epidemic.

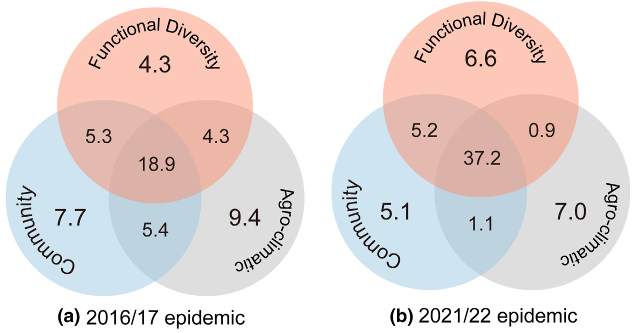

FIGURE 4 The results of variation partitioning analysis for the 2016/17 (a) and 2021/22 epidemics (b).

However, in the 2021/22 epidemic, the variation purely explained by functional diversity variables (6.6%) was comparable to those explained by agro-climatic variables (7.0%) or other community composition variables (5.1%).

DISCUSSION

Previous studies on the relationship between species' functional traits and pathogen diversity have primarily focused on pathogen richness while neglecting the diversity within a pathogen species. In addition, the effects of functional diversity on community-level infection risk have rarely been investigated in studies on the diversity–disease relationship. We here explored the associations of waterbirds' functional traits with their AIV host status and subtype richness at the species level, as well as the effects of community functional diversity on HPAI H5Nx occurrence at the community level. We demonstrated that both AIV host status and subtype richness were correlated with species' functional traits. In addition, the community functional diversity, including both traits' CWMs and community functional divergence, contributed to explaining the spatial patterns of HPAI H5Nx occurrence in wild birds.

AIV host status and subtype richness

AIV host status was negatively correlated with the age of sexual maturity, and subtype richness was positively correlated with clutch size. These results could be explained by life-history theory, which predicts higher susceptibility for fast-living species (i.e., with larger clutch size and earlier age of sexual maturity) because these species typically allocate more energy and resources in reproduction than in immune defences (Joseph et al., 2013; Valenzuela-Sánchez et al., 2021). These results are also consistent with previous studies on the susceptibility of birds to Eastern equine encephalitis virus (Huang et al., 2013) and the richness of zoonotic pathogens in rodents (Han et al., 2015). In addition, we also found that species with larger body mass were more likely to be AIV hosts, which seems apparently contradictory with predictions derived from the life-history theory that larger species may have a lower susceptibility due to their expected larger investments in immune defences. However, host status and pathogen diversity can be influenced by both species' exposure and susceptibility (Becker, Seifert, & Carlson, 2020; Downs et al., 2019; Merrill & Johnson, 2020). Although larger species may invest more in immune defences and thus be more resistant to infection, they may also be exposed more and accumulate more pathogens due to their larger size (and hence surface area), geographic range, or longevity (Smith et al., 2020). Indeed, we also found a positive correlation between longevity and subtype richness, consistent with a study that found birds with longer longevity were more likely to transmit vector-borne *Borrelia burgdorferi* to naïve ticks (Becker & Han, 2021). These results highlight the complexity of the life-history theory and indicate that future trait-based studies must consider all potential processes involved in pathogen transmission when investigating the effect of a trait.

Besides life-history traits, we found that, the hard-wing index (HWI), as a measure of dispersal ability, was positively correlated with both AIV host status and subtype richness, which could be explained by that species with higher dispersal ability may have a greater probability of pathogen exposure (Smith et al., 2021). Previous studies also suggested migration strategy can influence host exposure to pathogens (Teitelbaum et al., 2018). However, we here found that neither AIV host status nor subtype richness were significantly associated with migration strategy. Such results could be attributed to the fact that migration strategy might not be a good measure for dispersal in our study. In fact, only a few waterbird species (17 out of 143) in our study are sedentary species, possibly limiting ability to detect effects. Also, the strategies of full migration and partial migration might not reflect the dispersal ability at the species-level. More quantitative measures of migration strategy, such as migratory distance or dispersion (Gilroy et al., 2016), may be more informative.

In addition, we found that, after controlling for host phylogeny, invertebrate diet was positively correlated with AIV host status, while vertebrate diet was negatively correlated with subtype richness. In fact, species with vertebrate-based diets only accounted for 8.33% (4 out of 48) of the Anseriformes, which had the highest AIV subtype richness (Figure 1). The phylogenetic signal for and the effects of functional traits on host status and subtype richness suggest that the heterogeneity in waterbird AIV infection outcomes is determined by species-specific differences in physiological receptivity to AIV and in the functional traits that affect their exposure risks and immune response to infection.

Community functional diversity and HPAI H5Nx in wild birds

Our analyses of HPAI H5Nx occurrence at the community level demonstrated that the variables related to community functional diversity could efficiently explain the spatial patterns of H5Nx occurrence in both the 2016/17 and 2021/22 epidemics. In both epidemics, we found that the probability of H5Nx outbreaks was positively correlated with the CWMs of clutch size, and was negatively correlated with the proportion of solitary birds. In addition, the CWMs of body mass, HWI and plant seed diet also showed positive effects in the 2016/17 epidemic, while the CWMs of incubation time and invetebrate diet also showed negative effects in the 2021/22 epidemic. Considering that most of these traits also had similar effects on host status or subtype richness, our results suggest that the effects of functional traits on infection outcomes at the species level could scale up to affect pathogen transmission dynamics at the community level.

In addition to CWMs, several functional divergence metrics (i.e., MPD of foraging strata and MNTD of diet guilds in the 2016/17 epidemic, MPD of diet in the 2021/22 epidemic) were negatively correlated with H5Nx occurrence, which supports a possible dilution effect of community functional diversity. Previous studies also suggested a negative association between phylogenetic diversity metrics (i.e., phylogenetic MPD and MNTD) and the probability of H5Nx occurrence in wild birds (Huang et al., 2019). There are two potential mechanisms that could explain this negative correlation. First, AIVs may be more likely to transmit among closely related species due to their similar receptivity. Second, higher transmission risk might be caused by higher contact rates among closely related species, as they are more likely to congregate at similar habitats due to shared behavioural or physiological requirements (Fountain-Jones et al., 2018). A recent study found that the interspecific transmission of AIVs among wild birds in North America was negatively associated with the phylogenetic distance between hosts (Hicks et al., 2022), which confirmed the first mechanism. Importantly, our findings of negative effects for several functional divergence metrics provide support for the second mechanism. Our results therefore provide new insights into HPAI prediction and prevention. For example, several studies have suggested that degrading or recovering wetlands habitats are more likely to attract waterbirds with similar functional traits via the process of the environmental filtering (Li et al., 2019; Wang et al., 2022). Thus, these habitats may also have a higher HPAI risk, a prediction that could be tested in future studies.

We acknowledge that the H5Nx outbreak data collected from the FAO database may underestimate the true number of outbreaks due to the applied passive surveillance system. However, this database is one of the most comprehensive available data and has been widely used in previous studies mapping HPAI risk (Dhingra et al., 2016; Martin et al., 2011; Si et al., 2010, 2013; Tian et al., 2015). In addition, due to the availability of waterbird census data, the spatial extent of our study is relatively narrow, particularly in the context of current global HPAI outbreaks. Future studies are encouraged to test the generalization of our conclusions in other regions. For example, community science data derived from eBird (Sullivan et al., 2014) could be used to generate waterbird community data for more locations, though its spatial precision would be expected to be lower than those derived from the IWC wetland census data.

In summary, our work highlights the importance of trait-based approaches in understanding pathogen transmission at both the species and community levels. Our results suggest that both AIV host status and subtype richness, at the species level, are jointly determined by hosts' functional traits and phylogeny. At the community level, community functional diversity, including both the community-weighted means of functional traits and functional divergence, can contribute to explaining spatial patterns of H5Nx occurrence in wild birds. Importantly, the negative effect of functional divergence supports a dilution effect of community functional diversity. These results not only contribute to extend the current framework of the diversity-disease relationship, but also provide new insights for HPAI prediction and prevention.

AUTHOR CONTRIBUTIONS

SY, NL, and ZYXH designed research; SY, NL, and CL collected trait data; SY, WX, GH, LC collected AIV data; TM collected waterbird census data; SY, NL, WX, LC processed data; NL, DJB, and ZYXH performed phylogenetic comparative analyses; SY, WX and ZYXH performed logistic regression analyses; SY, DJB, WFdeB, CX, and ZYXH wrote the first draft, and all authors contributed substantially to revisions.

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DATA AVAILABILITY STATEMENT

Data of body mass, diet, and foraging strata were collected from the EltonTraits 1.0 database (Wilman et al., 2014). Data of longevity and age of sexual maturity were extracted from the AnAge databank (De Magalhaes & Costa, 2009). Data of migration strategy and hard-wing index were obtained from the AVONET databank (Tobias et al., 2022). Sociality data was extracted from (Møller, 2006). Clutch size, incubation time and dabbling behaviour data were extracted from Birds of the World: https://birdsoftheworld.org. HPAI H5Nx outbreak data was collected from FAO: http://empres-i.fao.org/eipws3g. Waterbird census data was collected from IWC Online database: http://iwc.wetlands.org. Climatic data (monthly temperature and precipitation) was collected from CRU databank (Harris et al., 2020). Poultry (chicken and domestic duck) density was calculated based on Gridded Livestock of the World (Gilbert et al., 2018). Waterbody data was collected from the Global Lakes and Wetlands Database (GLWD; Lehner & Döll, 2004). Human density was calculated based on Gridded Population of the World (GPW): http://sedac.ciesin.columbia.edu/data/collection/gpw-v4. All datasets used for analyses and R codes are archived in Figshare: https://doi.org/10.6084/m9.figshare.23549925.v2.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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