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Annual Global Habitat Maps of Avian Influenza Host Birds From 2000 to 2022

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ABSTRACT

Introduction and Aim: Long-term changes in wildlife habitats are fundamental for understanding biodiversity change and the ecological contexts that may shape opportunities for host contact or exposure. Avian influenza virus (AIV), one of the most pressing zoonotic threats, is maintained primarily in wild birds whose habitats are undergoing rapid transformation. Yet no globally consistent, temporally explicit habitat dataset tailored to AIV host species exists, leaving their long-term habitat dynamics poorly documented. To address this gap, we developed the first global annual habitat maps of AIV host birds from 2000 to 2022.

Main Variables Included: We developed a habitat classification framework specific to AIV host birds and produced the global annual terrestrial habitat maps by integrating satellite-derived land cover, climate zones, biome information and topography. The dataset includes 8 Level-1 and 34 Level-2 habitat types, achieving overall accuracies of 0.84 (± 0.08) and 0.83 (± 0.12), respectively.

Time Coverage: The maps span the years 2000–2022, with annual temporal resolution.

Spatial Coverage: The dataset covers global terrestrial surfaces (excluding Antarctica) at a resolution of 300 m.

Taxa: Wild bird species with confirmed AIV detections, with habitat preferences derived from IUCN species-level associations.

Applications: This dataset provides a foundational environmental layer for improving host species distribution models and for examining how environmental change influences habitats used by AIV host birds. It can support downstream ecological and epidemiological analyses within a One Health framework and inform conservation planning and land-use management.

1 | Introduction

Species' habitats have changed rapidly under global change including land-use conversion, climate variability and intensifying human activity (Tilman et al. 2017; Williams et al. 2022; Zheng et al. 2021). These transformations disrupt biodiversity patterns and reshape interactions among environments,

wildlife and humans. For zoonotic host species, such shifts can alter geographic distributions and movement patterns, thereby shaping opportunities for cross-species pathogen transmission (Carlson et al. 2022; Gibb et al. 2020). Avian influenza virus (AIV) stands out as the most likely zoonotic disease to cause the next global pandemic (Uyeki et al. 2017). Maintained primarily in wild bird reservoirs (The Global

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Consortium for H5N8 and Related Influenza Viruses 2016), AIV has repeatedly crossed species barriers and infected wild birds, poultry, mammals and humans (Agüero et al. 2023; Harvey et al. 2023; Leguia et al. 2023; Ramey et al. 2022; Xie et al. 2023). Because habitat change influences host abundance, occurrence and migratory behaviours, understanding the spatiotemporal dynamics of their habitats could provide an essential ecological basis for interpreting subsequent shifts in species distributions and potential exposure contexts within a One Health framework.

Habitat is broadly defined as the physical space that a species occupies or could potentially occupy within a specific spatial and temporal range, typically delineated by land cover and climate conditions (Kearney 2006). The International Union for Conservation of Nature (IUCN) Red List of Threatened Species classifies all habitat types associated with different species into a global habitat classification framework (IUCN 2012). Waterbirds, the primary natural host of AIV, predominantly inhabit aquatic environments such as wetlands, lakes and coastal regions (Gaidet et al. 2011; Xie et al. 2023; Yin et al. 2023). In addition to waterbirds, several terrestrial bird species have also been shown to be susceptible to AIV infection (Boon et al. 2007), suggesting that ecologically relevant host environments extend beyond aquatic habitats. Despite growing attention to species-environment interactions within conservation and disease ecology (Ellis 2021; Glidden et al. 2021; Millard et al. 2021; Outhwaite et al. 2022; Plowright et al. 2017), few studies have established a habitat classification framework tailored specifically to zoonotic hosts. Existing classification systems, such as the IUCN Habitat Classification Scheme, are developed for broad conservation goals and are not designed to capture ecological contexts relevant to pathogen transmission (IUCN 2012). Up to now, a systematic understanding of which habitat types are most ecologically relevant for AIV host birds remains lacking.

A further gap concerns the limited understanding of the spatiotemporal dynamics of AIV host bird habitats. Existing habitat mapping approaches have largely followed two pathways. The first, known as the Area of Habitat (AOH) (Lumbierres, Dahal, Soria, et al. 2022), refines IUCN range maps by removing unsuitable areas based on land cover and elevation. Although effective for narrowing species distributions, it does not explicitly delineate habitat nor capture temporal dynamics. The second approach maps habitat types directly based on land cover classifications (Jung et al. 2020), but these products are typically static, generalised across species, and not tailored to zoonotic hosts. As a result, they fall short in capturing temporal habitat transformations and in revealing how changing landscapes reshape spatial interfaces among wild hosts, domestic animals and humans. Furthermore, land cover-to-habitat translations often rely on predefined class definitions rather than empirical observations of species-specific habitat use, potentially misrepresenting the actual relationship between land cover and realised habitat. These limitations underscore the need for a host-focused habitat framework, as AIV host species occupy a distinct subset of habitat types compared with the broader avifauna. Existing global habitat products, therefore, lack the specificity required to capture the ecological settings most relevant to AIV maintenance.

Crucially, the lack of a globally consistent, temporally explicit habitat dataset for AIV host birds limits efforts to characterise long-term patterns in their habitat use and the environmental contexts relevant to potential host-pathogen interactions.

Here, we present the first annual global habitat maps of AIV host bird species from 2000 to 2022. We first develop the habitat classification system tailored to AIV host birds by integrating species-level habitat preferences from the IUCN Red List with confirmed host records from the Global Initiative on Sharing All Influenza Data (GISAID) (Shu and McCauley 2017), capturing the full diversity of ecological settings used by host species across life stages and seasons. Building on this framework, we then generate global, annually resolved terrestrial habitat maps for the period 2000–2022. Validation using eBird occurrence records, alongside cross-comparisons with existing habitat products, demonstrated strong temporal consistency and ecological fidelity across habitat types. This dataset fills a critical knowledge gap by providing, for the first time, globally consistent and temporally explicit habitat information for AIV host bird species. It offers a foundational environmental layer to improve host species distribution modelling and support downstream analyses of how environmental change affects host distributions and the ecological settings that may influence opportunities for exposure, contributing to broader One Health efforts to understand the ecological contexts of zoonotic emergence.

2 | Methods

2.1 | Overview

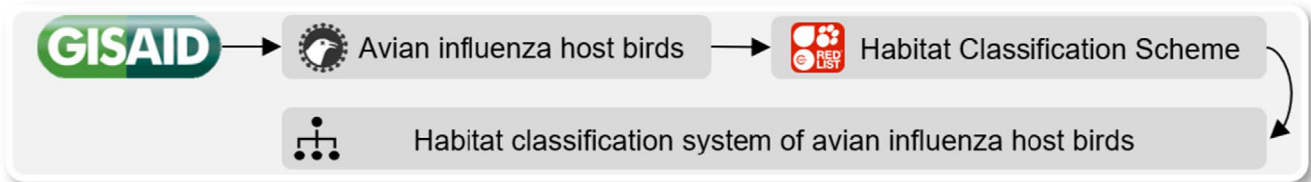
This study develops a comprehensive framework for generating and analysing annual terrestrial habitat maps of AIV host birds (Figure 1). We first establish a two-level habitat classification system by combining AIV host species records from the GISAID (Shu and McCauley 2017) with the habitat preference information from the IUCN classification scheme (IUCN 2012). Based on this framework, we produce annual habitat maps (2000–2022) by translating satellite-derived land cover datasets into habitat classes using a decision tree model. Additional environmental variables—including climate zones, biome types, elevation and alpine and mountain layers—are incorporated to improve spatial delineation of habitats. We validate the resulting maps through accuracy assessment using species occurrence data and by cross-comparing them with existing habitat products.

2.2 | Datasets

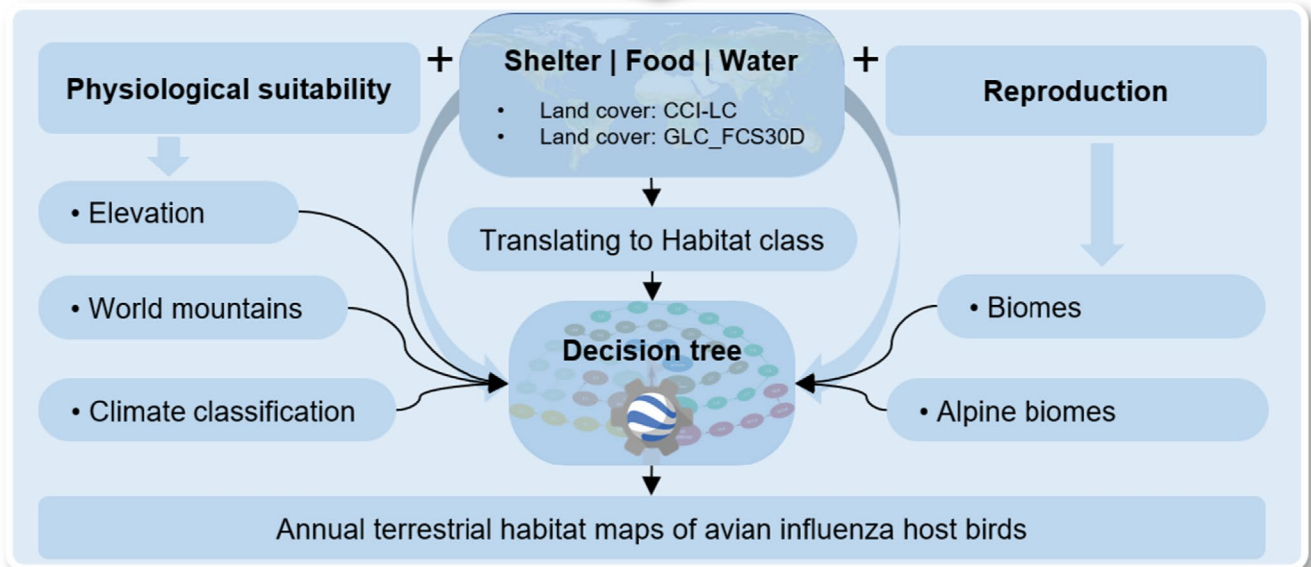
2.2.1 | List of Host Bird Species

This study focuses on bird species currently known to host influenza A viruses. Host information for these viruses was obtained from the GISAID, one of the largest platforms for sharing influenza-related data worldwide (Shu and McCauley 2017). GISAID serves as a key repository of genomic sequences and metadata on all influenza viruses and has been extensively utilised in One Health research (Forster et al. 2020; Gangavarapu et al. 2023; McBride et al. 2023; Mercatelli and Giorgi 2020;

1. Define classification system



2. Generate annual habitat maps



3. Data validation



4. Spatial-temporal analysis

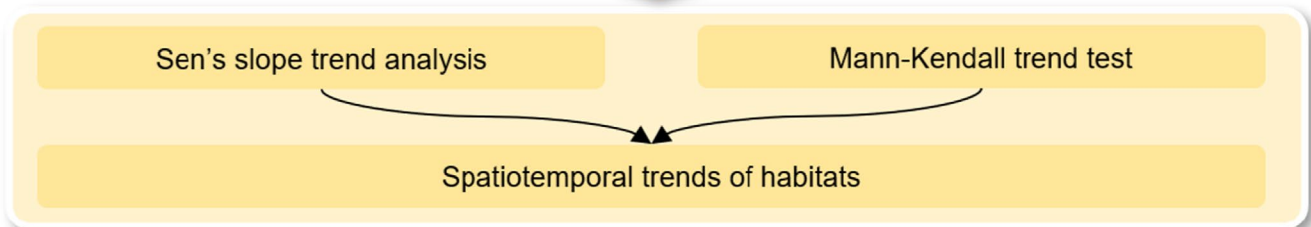


FIGURE 1 | Workflow of the study. GISAID stands for the Global Initiative on Sharing All Influenza Data.

Oude Munnink et al. 2020; Shi et al. 2018). From GISAID, we retrieved detailed information on the influenza A virus collected from 1973 to 2023, with a specific focus on the 'hostname' metadata to identify host species. Following data curation and validation, we confirmed a total of 300 bird species as AIV host bird species.

2.2.2 | Habitat Preference of AIV Host Bird Species

Habitat preference data for each species were provided by the IUCN Red List, which provides information on the 'Habitat types', 'Season', 'Suitability' and 'Major importance'. The IUCN Habitats Classification Scheme accounts for biogeographic factors, latitudinal zonation and depth in marine systems,

categorising habitats into 18 Level-1 and 100 Level-2 classes (IUCN 2012). For migratory birds, IUCN also provides information on seasonality of habitat use, distinguishing between 'Resident', 'Breeding', 'Non-breeding', 'Passage' and 'Unknown' categories. 'Suitability' reflects the extent to which a habitat supports a given species. 'Suitable' indicates that the species frequently inhabits the habitat; 'Marginal' suggests occasional presence or low population density. 'Unknown' denotes uncertainty regarding habitat suitability. Additionally, 'Major importance' assesses the relevance of each habitat for the species: if a habitat is deemed suitable, the 'Major importance' field shows a 'Yes' or 'No'. 'Yes' signifies that the habitat is crucial for the species' survival, either due to its essential role at a specific life stage (such as breeding or providing food resources) or because it serves as the primary habitat where most individuals occur.

2.2.3 | Satellite-Derived Land Cover Data

The primary land cover data used in this study is the European Space Agency Climate Change Initiative land cover (CCI-LC) product. CCI-LC provides a global dataset consisting of 22 classes at a 300-m resolution, updated annually since 1992, and classified according to the United Nations Food and Agriculture Organization's (UN FAO) Land Cover Classification System (LCCS) (Defourny et al. 2017). To refine land cover information, we incorporated GLC_FCS30D, which provides greater detail on wetland subcategories such as inland wetlands (swamp, marsh, flooded flat and saline) and coastal wetlands (mangrove, salt marsh and tidal flat) (Zhang et al. 2024). GLC_FCS30D is the first global dataset for monitoring land cover dynamics at a 30-m resolution, covering 35 land cover subcategories and spanning the period from 1985 to 2022 (Zhang et al. 2024).

2.2.4 | Translation Table From Land Cover to Habitat Class

The translation table linking IUCN habitat class and land cover types was obtained from Lumbierres, Dahal, Di Marco, et al. (2022). This dataset was derived from a data-driven model based on point locality data for birds. Lumbierres, Dahal, Di Marco, et al. (2022) extracted the land-cover class for each point locality and aligned them with the corresponding IUCN habitat class, employing logistic regression models to quantify habitat-land cover associations. The model-generated odds ratios were then used to assess the strength of the association between habitat types and land cover. The classification accuracy between habitat class and land cover from CCI-LC is 71.1%. To ensure high confidence in our habitat classification, we only included habitat-land cover associations where the odd ratio ≥ 1.396 , as increasing the threshold reduced the presence of spurious associations (Table S1).

2.2.5 | Climate and Biome Zoning Data

To characterise the climatic conditions of the habitats, we utilised climate zones defined by the Köppen-Geiger climate classification system (Beck et al. 2018). This dataset, available at 1-km resolution, represents contemporary climate conditions (1980–2016) and was generated from a combination of four high-resolution, terrain-corrected climate datasets, offering improved classification accuracy and greater detail compared to previous versions. Additionally, we incorporated global alpine biome data and realm delineations to refine habitat classifications and generate masks for distinguishing between subtropical and tropical regions (Dinerstein et al. 2017; Testolin et al. 2020).

2.2.6 | Mountain Maps and Elevation Data

To differentiate lowland and mountain habitat classes, we employed the K1 mountain map (Roger et al. 2018) and digital elevation model (DEM) from the NASA Shuttle Radar Topography Mission (SRTM) (Jarvis et al. 2008). The

K1 mountain map, produced by the World Conservation Monitoring Centre, is the first global and objective description of mountainous characteristics, classifying mountains into six categories based on a combination of elevation and relative topography. It reveals that 26.4% of the Earth's terrestrial surface is mountainous (Roger et al. 2018). The SRTM DEM features high spatial resolution and accuracy, with a spatial resolution of approximately 90 m at the equator and a vertical error of less than 16 m (Jarvis et al. 2008).

2.3 | Defining the Habitat Classification System of AIV Host Bird Species

The IUCN Habitats Classification Scheme comprises 18 Level-1 and 100 Level-2 habitat classes. However, not all habitat types are relevant for AIV host birds. To establish a suitable classification system, we integrated habitat preference data from the IUCN Red List with the AIV host bird list from GISAID, generating a host-habitat association framework. For each species, we considered habitat preferences across four seasonal periods: Resident, Breeding, Non-breeding and Passage. To ensure the reliability of habitat classification, we excluded habitats categorised as 'Marginal' or 'Unknown' in terms of suitability, as well as those where 'Major importance' was marked as 'No', given their higher uncertainty in representing essential habitats. Marginal-use habitats constitute only a small fraction of all host-habitat associations and always occur alongside suitable habitats (Table S2). Their exclusion, therefore, has negligible influence on the resulting habitat classification system. Based on these host-habitat associations, we derived a refined habitat classification system specifically for AIV host bird species, ensuring ecological relevance and applicability for mapping their distributions.

2.4 | Generating Annual Habitat Maps of AIV Host Bird Species

We employed a decision tree method (Jung et al. 2020) to integrate land cover, climate and ecological datasets, enabling a systematic classification of each habitat type (Figure 2). The mapping process was conducted in two stages. First, we delineated the spatial extents of all Level-1 habitat categories using constraints specified in the habitat-land cover translation table, along with criteria for physiological and reproductive suitability (Table S1). Next, within the defined boundaries of each Level-1 habitat, we mapped the distribution of their corresponding Level-2 habitat types. To maintain spatial consistency, all input datasets were resampled to a 300-m resolution, aligned with the CCI-LC dataset. The hierarchical mapping followed a strict, pre-defined sequence based on previous studies (Jung et al. 2020). At the Level-1 classification stage, artificial habitats were prioritised, subsequently masking deserts, which in turn masked forests, and so forth. For Level-2 classification, a similar hierarchical approach was applied. For example, the 'forest-subtropical/tropical moist montane (1.9)' was mapped first, followed by 'forest-subtropical/tropical mangrove vegetation above high tide level (1.7)'. To reduce misclassification errors in Level-2 habitat types and improve consistency in habitat delineation, certain Level-2 habitat

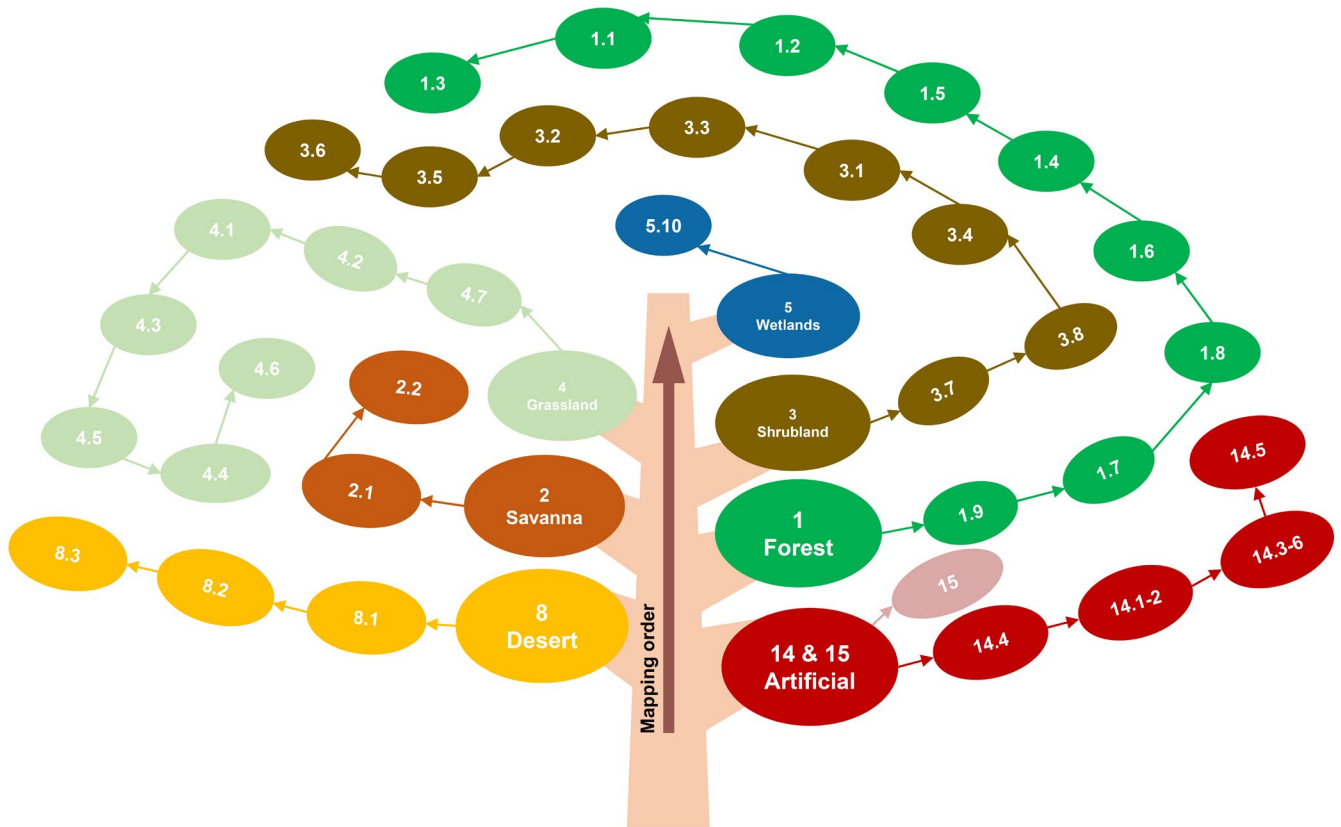


FIGURE 2 | The sequence of decision trees for generating habitat at Level-2 of the AIV host bird species. Different colours represent the Level-1 habitat classes. The arrows indicate the mapping order of each Level-2 habitat class, following the approach of Jung et al. (2020). Artificial habitat classes (red and pink) are masked out from all other habitat classes.

types were aggregated such as artificial arable land (14.1) and artificial pastureland (14.2). These adjustments were driven by the classification granularity of the land cover dataset and the constraints defined in the habitat-land cover translation table (Defourny et al. 2017; Lumbierres, Dahal, Di Marco, et al. 2022).

2.5 | Data Validation

2.5.1 | Independent Accuracy Assessment Based on eBird Observations

To assess the accuracy of each habitat class at both classification levels, we first identified bird species with a single habitat preference at the Level-1 and Level-2 classifications based on the IUCN Red List, totaling 2891 and 1518 species, respectively. We then retrieved bird presence records for these selected species from eBird, a global citizen science platform that collects bird observation data contributed by volunteers worldwide (Sullivan et al. 2009). To minimise potential biases of the eBird data from survey methodology and effort, we applied strict data quality filters, following established protocols from previous studies (Johnston et al. 2021; Kelling et al. 2015). These include complete checklists, stationary or travelling protocols, survey durations under 5 h, travel distances under 3 km, and fewer than 10 observers per checklist. These filters help reduce variability, ensuring consistent species detection rates and improving data reliability. Finally, a total of 2445 single-habitat species remained

for validation, contributing 45,499,366 presence records globally (Figure S1).

Validation was performed at the pixel level. A pixel was considered correctly classified when at least one presence record of a single-habitat species occurred within it, and the species' sole IUCN-defined habitat matched the pixel's assigned habitat type. For each species, we calculated the proportion of presence points that fell within the corresponding habitat class at both classification levels as an accuracy metric, respectively. The accuracy was calculated using the following formula:

$$\text{Accuracy} = \frac{n_{\text{withinHabitat}}}{n_{\text{All}}} \quad (1)$$

where $n_{\text{withinHabitat}}$ denotes the number of species occurrence points (from eBird) falling within the corresponding mapped habitat, and n_{All} is the total number of species occurrence points.

2.5.2 | Comparison With Habitat Maps Developed by Jung et al. (2020)

At the global scale, publicly available species habitat datasets remain highly limited. The habitat product developed by Jung et al. (2020) is the only dataset that exhibits some degree of similarity to ours. To assess the consistency between the two

datasets, we first calculated the proportion of each habitat type within 1-degree grid cells for both datasets. We then performed a correlation analysis, comparing each habitat class at both classification levels in our 2015 habitat product with the corresponding categories in Jung et al. (2020)'s dataset. A higher correlation indicates greater similarity between the two datasets, whereas a lower correlation suggests discrepancies in habitat classification.

2.6 | Trend Analysis of Habitats

We quantified long-term changes in habitat availability by analysing trends in each Level-1 habitat type for the period 2000–2022. For each year, the global Level-1 habitat map was reclassified to isolate the focal habitat class, and the annual layers were then aggregated to a common 50×50 km grid so that each grid cell represents the proportion of area covered by that habitat type in that year. The resulting annual time series for each grid cell was used to estimate linear trends in habitat proportion over time. To evaluate whether the observed trends were statistically meaningful, we applied a Mann-Kendall test to each grid-cell time series and retained only trends with $p \leq 0.05$. The final trend maps summarise the direction and magnitude of change for each habitat type and form the basis for describing global spatiotemporal patterns of habitat dynamics in this study.

3 | Results

3.1 | Habitat Classification System of AIV Host Bird Species

AIV host birds are associated with 12 of the 18 Level-1 habitat classes (66.7%) and 77 of the 100 Level-2 habitat classes (77%) defined in the IUCN Habitat Classification Scheme (Figure 3 and Table S3). The terrestrial habitats encompass 8 Level-1 classes including forest, savanna, shrubland, grassland, wetlands, desert, artificial-terrestrial and artificial-aquatic habitats (Figure 3A). Within these Level-1 classes, there are 56 Level-2 habitat types (Figure 3B and Table S3). Among these habitats, wetlands support the highest number of AIV host species, with 198 species, accounting for 66.0% of all known host species. Artificial terrestrial habitats and grasslands follow, comprising 41.3% and 38.7% of host species, respectively. For marine habitats, AIV host birds predominantly occupy four habitat types including marine neritic, marine oceanic, marine intertidal and marine coastal/supratidal (Figure 3A). Most host birds are concentrated in neritic, tidal and coastal areas (Figure 3B). Across the full IUCN Habitat Classification Scheme, 6 Level-1 classes (Inland Rocky Areas; Caves and Subterranean Habitats; Marine-Deep Ocean Floor; Introduced Vegetation; Other; Unknown) and 23 Level-2 classes show no documented use by any confirmed AIV host birds and are therefore excluded from the mapped habitat framework.

3.2 | Evaluations of the Derived Habitat Maps

The mapped habitat classes showed high classification accuracy when evaluated against single-habitat species occurrences.

A pixel was considered correctly classified when at least one presence record of a species whose sole IUCN-defined habitat matched the pixel's assigned habitat type occurred within it. The average accuracy of the Level-1 and Level-2 habitat maps was $0.84 (\pm 0.08 \text{ SD})$ and $0.83 (\pm 0.12)$, respectively (Figure 4). However, accuracy varied across different habitat types (Figure 4A). Among Level-1 habitats, forest exhibited the highest average accuracy (0.90 ± 0.03), whereas shrublands had the lowest accuracy (0.76 ± 0.05). The accuracy estimates for other Level-1 habitat classes were as follows: savanna (0.87 ± 0.08), grassland (0.84 ± 0.08), wetlands (0.86 ± 0.07), desert (0.82 ± 0.06), artificial-terrestrial (0.82 ± 0.07) and artificial-aquatic (0.83 ± 0.09).

In addition to differences among habitat types, accuracy also exhibited interannual variability across the 23 years (Figure 4A). This fluctuation occurs to some extent in most habitat classes due to annual differences in the underlying land-cover products, whereas it is most pronounced in water-related habitats such as wetlands and artificial-aquatic environments. These habitats experience strong seasonal and interannual fluctuations in hydrology, which introduce spectral variability and increase classification uncertainty, leading to larger year-to-year changes in accuracy.

Moreover, Level-2 habitat maps consistently showed lower accuracy than Level-1 maps (Figure 4B). This reduction is expected because Level-2 classes represent more fine-grained ecological distinctions and therefore exhibit higher spectral similarity and greater potential for misclassification in satellite-based products.

At Level-2 classes, 30 out of the 34 mapped habitat classes could be validated, as species presence data were available for bird species with a single habitat preference corresponding to these habitat types (Figure 4B). Forest-related habitats exhibited consistently high classification accuracy, ranging from 0.76 to 1.00. In contrast, grassland and desert habitats showed lower accuracy, with overall accuracy ranges of 0.75–0.89 and 0.72–0.84, respectively. Among other habitat categories, artificial habitats demonstrated relatively high classification accuracy at Level-2, with accuracy values ranging from 0.84 to 0.90. Our product also shows good agreement with the 2015 habitat maps developed by Jung et al. (2020) (Figure S1). These results underscore both the strengths and limitations of the habitat classification approach. Certain habitat types benefit from well-defined spectral characteristics, enhancing classification accuracy. However, others—particularly those influenced by seasonal or interannual variability—pose greater classification challenges. Recognising these variations is essential for refining habitat classification methodologies and ensuring long-term consistency in habitat mapping.

3.3 | Spatial Pattern of AIV Host Bird Habitats in 2022

We successfully generated terrestrial habitat maps for AIV host bird species, identifying 8 Level-1 and 34 Level-2 habitat classes. Natural habitats—including forest, savanna, shrubland, grassland, wetlands and desert—constituted 77.6% of the total terrestrial habitat area in 2022, whereas artificial habitats—comprising

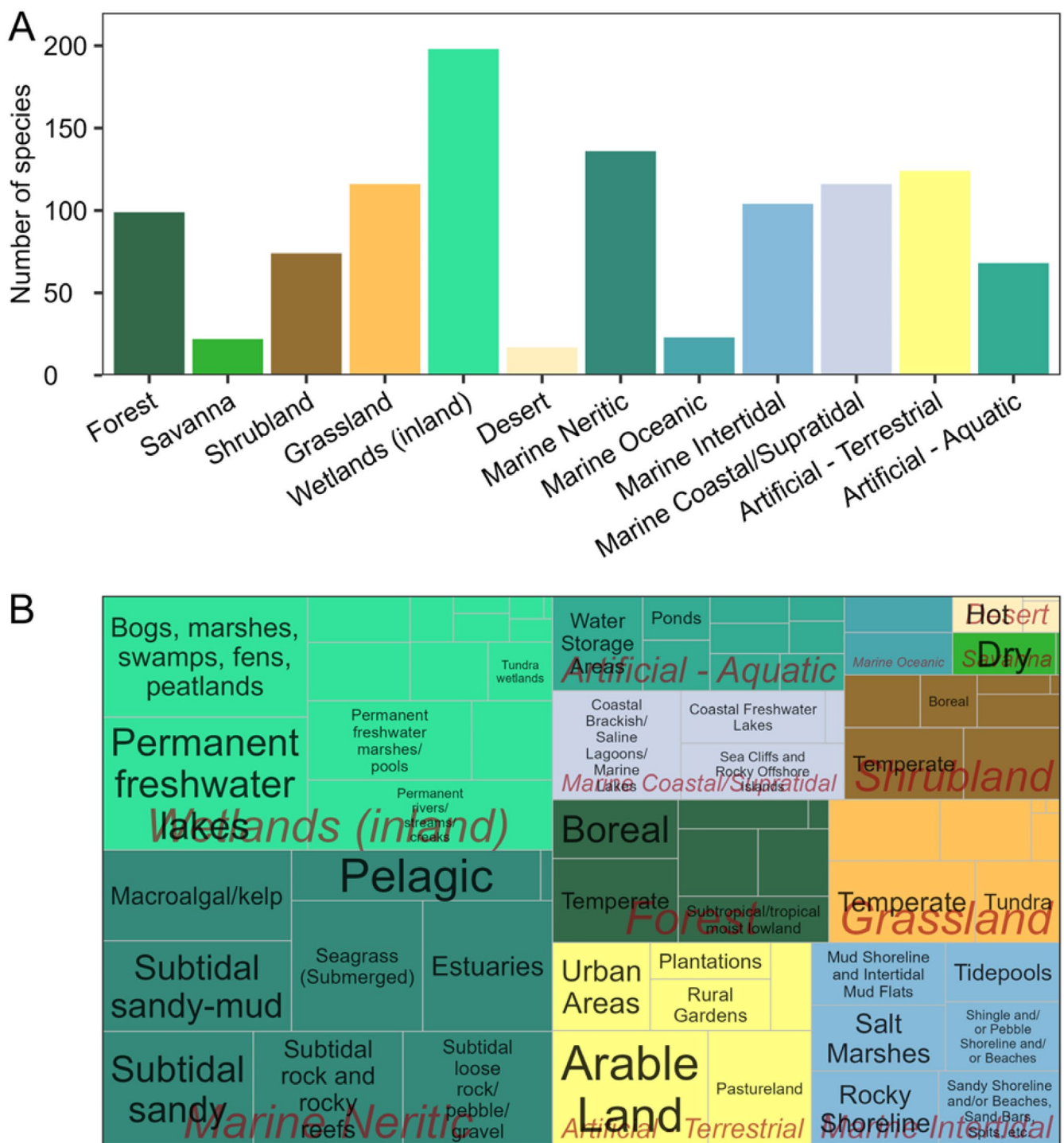


FIGURE 3 | Summary of habitat classes for AIV host bird species. (A) The number of AIV host bird species in habitat classes at Level-1. (B) The habitat classes at Level-2 of the AIV host bird species. Red names represent Level-1 habitat classes, whereas black names indicate Level-2 habitat classes. The colour area is proportional to the number of species in (A). It should be noted that the Level-2 habitat classes with smaller proportions are not shown.

artificial-terrestrial and artificial-aquatic—accounted for 22.4% (Figure 5). Among natural habitats, forest, desert and grassland covered the largest areas, representing 28.9%, 18.4% and 11.5% of the total, respectively. Other natural habitat types each contributed less than 10%, with wetlands and shrublands both comprising 7.6% and savanna making up 3.5%. For artificial habitats, the area of artificial-terrestrial is over eight times larger than that of

artificial-aquatic (20.0% vs. 2.4%). The dominant artificial habitat types included artificial arable & pasture lands (14.1 and 2) and artificial degraded forest & plantations (14.3 and 6). These habitats were predominantly distributed across the North China Plain, the Indo-Gangetic Plain, the Central Great Plains of the United States, Ukraine and the Pampas Steppe of Argentina (Figure 5).

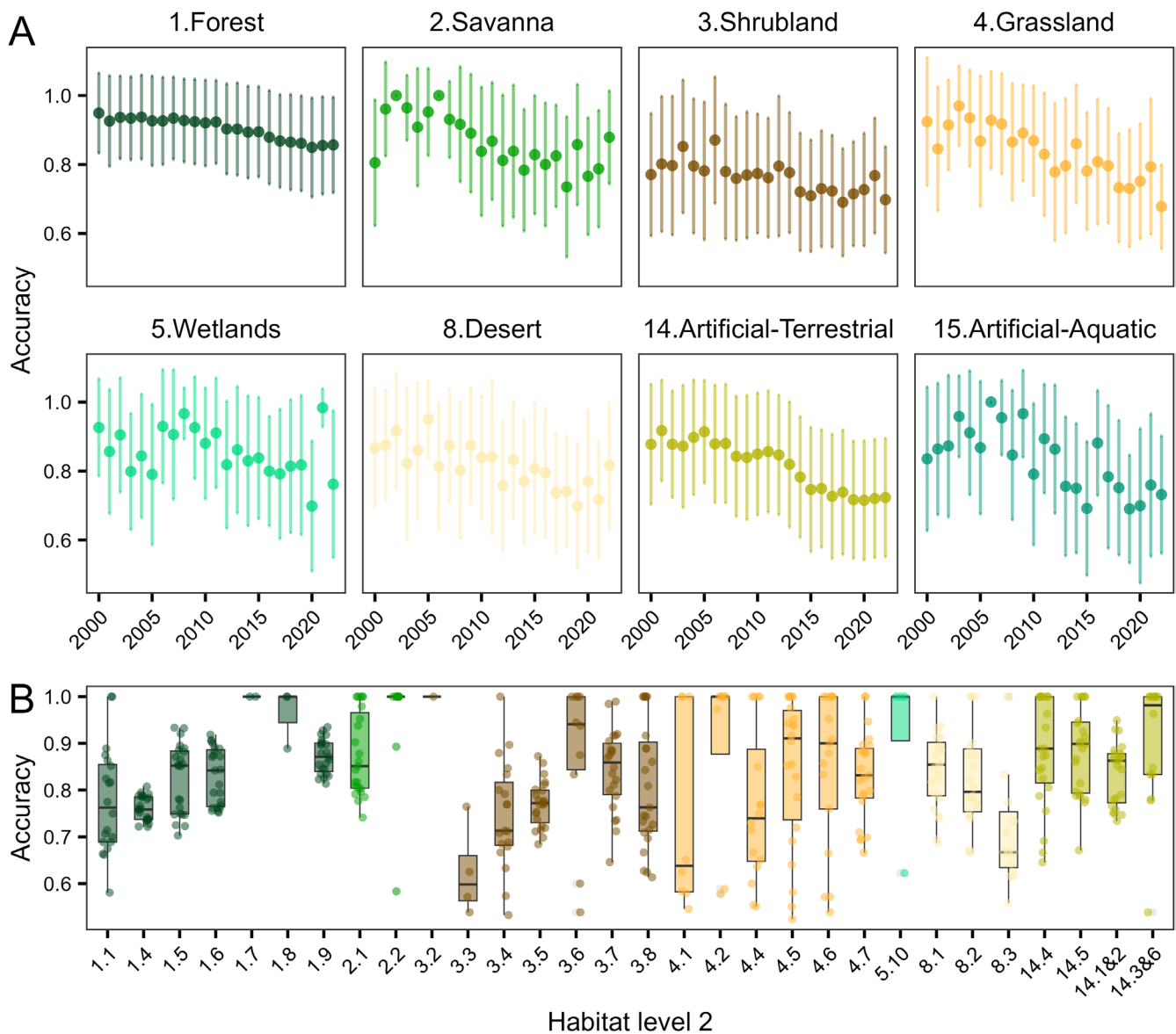


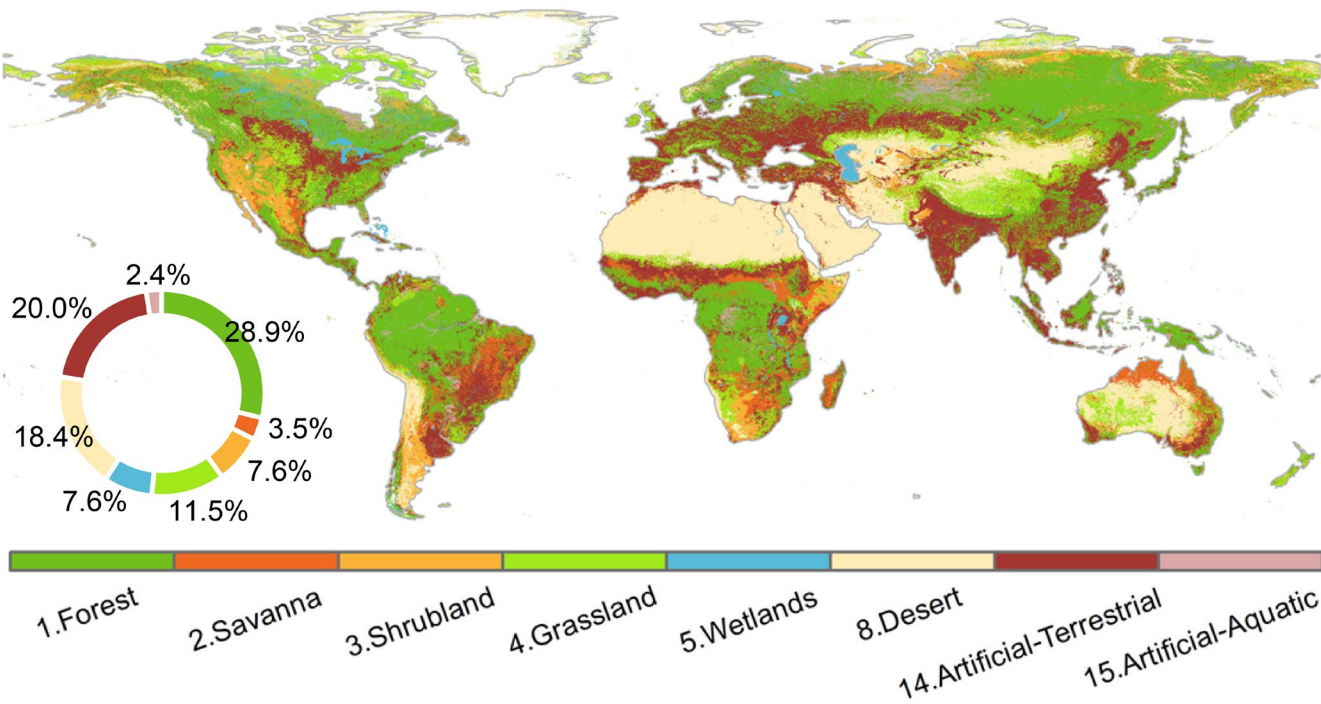
FIGURE 4 | Accuracy assessment for the Level-1 and Level-2 habitat maps. (A) Accuracy of the Level-1 habitat types across different years. Each point represents the mean accuracy of a given habitat type in a specific year, with error bars indicating one standard deviation, calculated based on the mean accuracy of all species that exclusively prefer this single habitat type. (B) Accuracy of Level-2 habitat types. Each point in the boxplot represents the mean accuracy of all species that exclusively prefer the given habitat type in a specific year.

3.4 | Spatiotemporal Patterns of AIV Host Bird Habitats

To characterise the long-term habitat dynamics, we quantified linear trends in the proportion of each Level-1 habitat type within 50×50km grid cells from 2000 to 2022 (Figure 6). The resulting maps reveal substantial spatial heterogeneity, with distinct regions of expansion and contraction across habitat types. Forest habitats show major declines across the Amazon, Central Africa and Southeast Asia, with increases in parts of Europe, sub-Saharan Africa and southwestern China. Savanna habitats decline broadly in sub-Saharan Africa, with localised gains in central South America. Shrubland habitats increase widely across northern North America and northern Eurasia and decline in Australia, Central Asia and the Mediterranean. Grassland habitats decrease across the North American Great

Plains and eastern China, whereas increases occur in Mongolia and Central Asia. Wetland habitats show general declines across northern North America, northern Eurasia and Europe, alongside scattered increases in tropical and temperate regions. Desert habitats increase across the Middle East, Central Asia and western Australia, with limited declines in adjacent managed drylands. Artificial-Terrestrial habitats expand markedly across South and Southeast Asia, eastern China, and parts of Africa and South America, with declines concentrated in temperate Europe and selected regions of Africa and South America. Artificial-aquatic habitats increase in Northeast Asia and decline across northern Eurasia and from central to northern North America. These spatially explicit patterns demonstrate substantial and heterogeneous reconfiguration of habitats relevant to AIV host species over the past two decades, highlighting the value of the annual maps for assessing global habitat change.

A. Level 1 habitat class



B. Level 2 habitat class

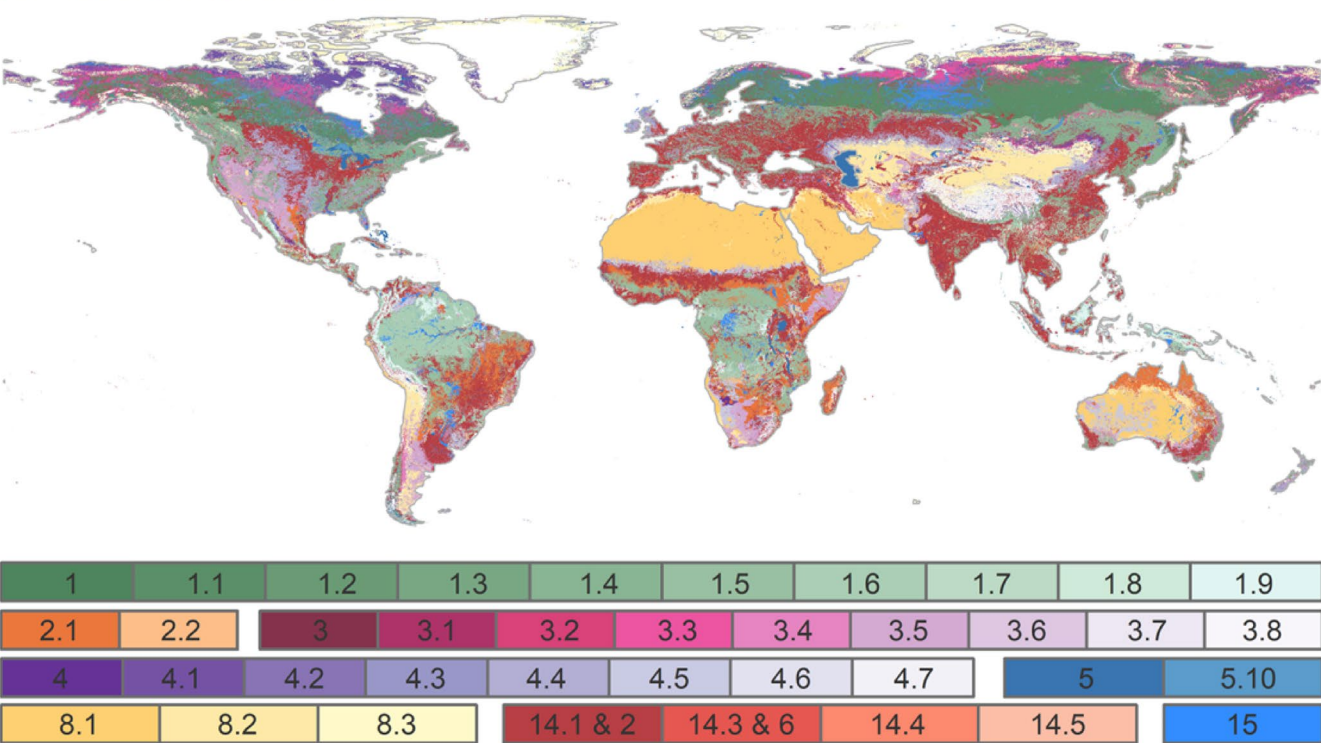


FIGURE 5 | Spatial distribution of AIV host bird habitats in 2022. (A) Spatial distribution of Level-1 habitat classes. The subplots represent the proportions of each Level-1 class. (B) Spatial distribution of Level-2 habitat classes. The numbers in the legend represent the codes for each Level-2 class. For more detailed information, please refer to Table S3.

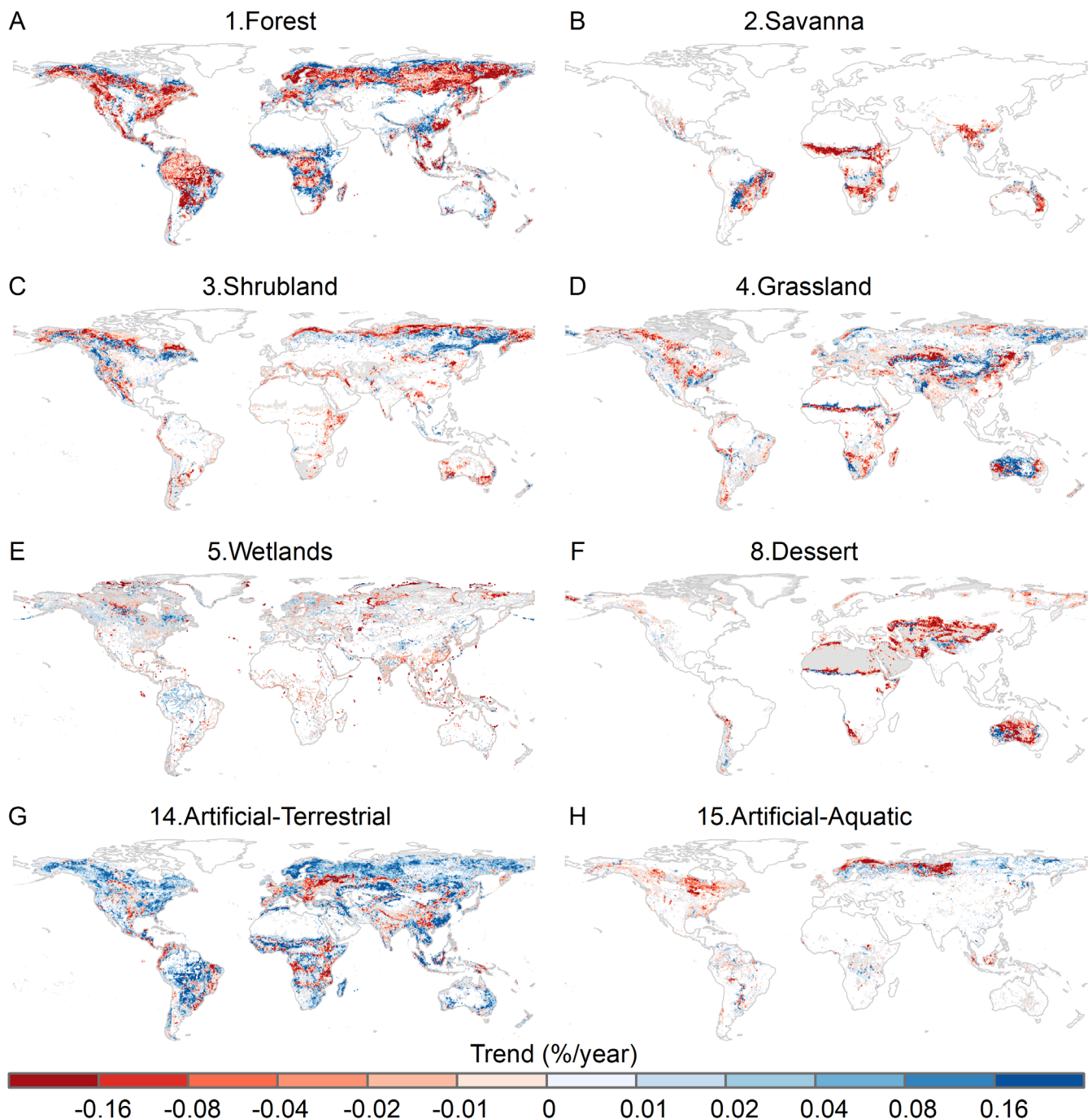


FIGURE 6 | Spatial patterns of trends in Level-1 habitats at 50 km × 50 km grid cells for AIV host bird species during 2000–2020. The blue, red and grey areas indicate significant increases, significant decreases and no significant changes in the corresponding habitat classes, respectively.

4 | Discussion

4.1 | Potential Applications

The annual global habitat maps of AIV host bird species developed in this study provide a foundational resource for ecological and conservation research. By offering ecologically relevant and temporally explicit habitat information, these maps could improve species distribution modelling for AIV host bird species and help contextualise regions where opportunities for host contact or exposure may arise. Importantly, these habitat maps represent only one component of the broader spillover process.

Their value for spillover-related research emerges when they are combined with independent information on host abundance, movement, competence, or epidemiological data, enabling more comprehensive assessments of the environmental settings associated with transmission risk.

Beyond applications in disease ecology, this dataset enables examinations of how wetland loss, agricultural expansion and conservation policies shape long-term habitat availability for AIV host bird species. These insights may aid policymakers in balancing land-use development, biodiversity conservation and biosecurity priorities.

More broadly, by linking remote sensing with ecological and epidemiological datasets, these habitat maps contribute to a stronger environmental foundation for One Health research. The methodology framework is transferable to other host taxa or pathogen systems, supporting global monitoring efforts and the development of early warning indicators under changing environmental conditions.

4.2 | Study Limitations

This study also has several limitations that warrant consideration in future work. First, not all AIV host bird habitats could be comprehensively mapped. The habitat classification in this study relies heavily on remote sensing-based land-cover products (CCI-LC) and auxiliary environmental data. This dependence is particularly evident in wetland classifications, such as 5.4 and 5.7, which are inherently difficult to delineate using remote sensing-based approaches due to their high temporal variability and hydrological dynamics (Lumbierres et al. 2017; Mahdavi et al. 2018). Global-scale remote sensing products often fail to capture small ponds, ephemeral wetlands, or seasonally inundated areas, leading to potential underrepresentation of critical wetland habitats (Klein et al. 2017; Pekel et al. 2016). Consequently, some avian influenza host birds that rely on specific habitat preferences may have incompletely characterised habitat distributions in the dataset. These uncertainties may further influence downstream applications involving AIV exposure or spillover-related analyses, particularly those sensitive to fine-scale hydrological conditions such as modelling host congregation, migration stopover suitability or environmental virus persistence. Users should exercise caution when applying wetland-related habitat layers and, where possible, complement them with higher-resolution or regionally calibrated hydrological datasets.

Furthermore, although seasonal information was incorporated into the species-habitat association framework, the present study does not provide seasonally explicit habitat maps. This limitation stems from the dependence of our classification approach on global land-cover products such as CCILC and GLC_FCS30D, which are available only as annual composites and do not offer seasonal or intra-annual land-cover information. As a result, the habitat maps produced here necessarily reflect annual habitat availability rather than seasonal habitat dynamics. The seasonal information used during the association process serves solely to identify ecologically relevant habitat types for each species and should not be interpreted as representing seasonal species distributions. With continued advancements in remote sensing technologies and the development of higher-temporal-resolution land-cover products, future research may enable the production of seasonally resolved global habitat maps that would complement the annual layers presented here and better support analyses requiring season-specific habitat information for migratory AIV host species.

Third, the accuracy and resolution of the land-cover products and auxiliary data sources directly influence the reliability of the derived habitat maps. The CCI-LC dataset, which serves as the primary land cover input, has an overall classification accuracy of

71.1% (Defourny et al. 2017), whereas the GLC_FCS30D dataset exhibits a reported accuracy of 80.88% (Zhang et al. 2024). These uncertainties inherently propagate into the final habitat classifications, particularly for habitat types that share spectral similarities or occur in heterogeneous landscapes. Misclassification errors in the base land-cover data can introduce spatial inconsistencies in habitat representation, which may affect downstream ecological analyses and risk assessments.

Finally, validating annual habitat maps at a global scale presents significant challenges. Our validation approach relies on eBird presence records, which offer an extensive crowdsourced dataset for bird observations (Sullivan et al. 2009). However, species misidentifications, observer biases and heterogeneous survey efforts introduce unavoidable uncertainties. In addition, some species may occasionally be recorded in suboptimal or non-preferred habitats, either due to observation error or temporary habitat use during migration or periods of resource scarcity. Although stringent quality control filters were applied, such sources of noise cannot be fully eliminated. Moreover, because eBird provides presence-only observations, true absences cannot be reliably inferred, preventing a formal assessment of absence accuracy—that is, whether pixels mapped as non-focal habitats correctly represent areas where a species is truly absent. Conducting such assessments would require standardised survey data, which are not available at a global scale. For these reasons, our validation focuses on presence-supported consistency between mapped habitat classes and species known to specialise in those habitats.

Despite these limitations, the dataset provides valuable information for analysing avian influenza host bird habitat dynamics, supporting disease risk assessments, and informing land use and conservation policies. Future versions of this work could further improve habitat classifications by incorporating higher-resolution remote sensing products, enhanced modelling frameworks, and additional region-specific validation datasets, thereby strengthening the accuracy and utility of global habitat mapping for AIV host species.

Author Contributions

Q.Z., J.D., Z.L. and K.M. conceptualised the study. Q.Z. conducted all the analysis and drafted the initial manuscript. All authors contributed to the interpretation of results and the revision of the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The dataset and associated scripts are openly available at <https://figshare.com/s/d6dc7691d66923ea7154>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Global spatial coverage of eBird occurrence records used for habitat validation. **Figure S2:** Correlation between our habitat maps and Jung et al. (2020)'s maps in 2015. **Table S1:** Adapted translation table from land cover to habitat class according to Lumbierres et al. (2022). **Table S2:** Summary statistics of 'suitable' and 'marginal' habitat suitability across IUCN habitat classes for confirmed host species. **Table S3:** The habitat classification system for avian influenza host birds.