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## Short Communication

# Anthropogenic transformation in terrestrial habitats of avian influenza host birds in the 21st century

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Habitat change is a major driver of biodiversity loss and is increasingly linked to the emergence of zoonotic infectious diseases [1]. Avian influenza virus (AIV) represents a particular concern [2] because of its capacity to cross species barriers and infect wild birds, poultry, mammals, and humans [3,4]. Wild birds serve as the primary natural reservoirs of AIV, and their high mobility and long-distance migrations make them key agents of viral dispersal [5]. Alterations in their habitats may reshape movement patterns and elevate opportunities for contact with other hosts, with important consequences for viral persistence and transmission [6]. Yet despite increasing recognition of habitat transformation, the spatiotemporal dynamics of AIV host bird habitats have not been systematically evaluated. Addressing this gap is essential for understanding how environmental change is restructuring host landscapes and for providing a spatial foundation to support targeted conservation, land-use planning, and One Health interventions.

In this study, we tracked global habitat changes from 2000 to 2022 for AIV host bird species, defined as those with documented influenza A virus detections in the Global Initiative on Sharing All Influenza Data (GISAID) [7] (Supplementary material). Because this host list is derived from available GISAID surveillance records, some uneven representation across species is expected; nevertheless, the documented hosts collectively span all major IUCN Level-1

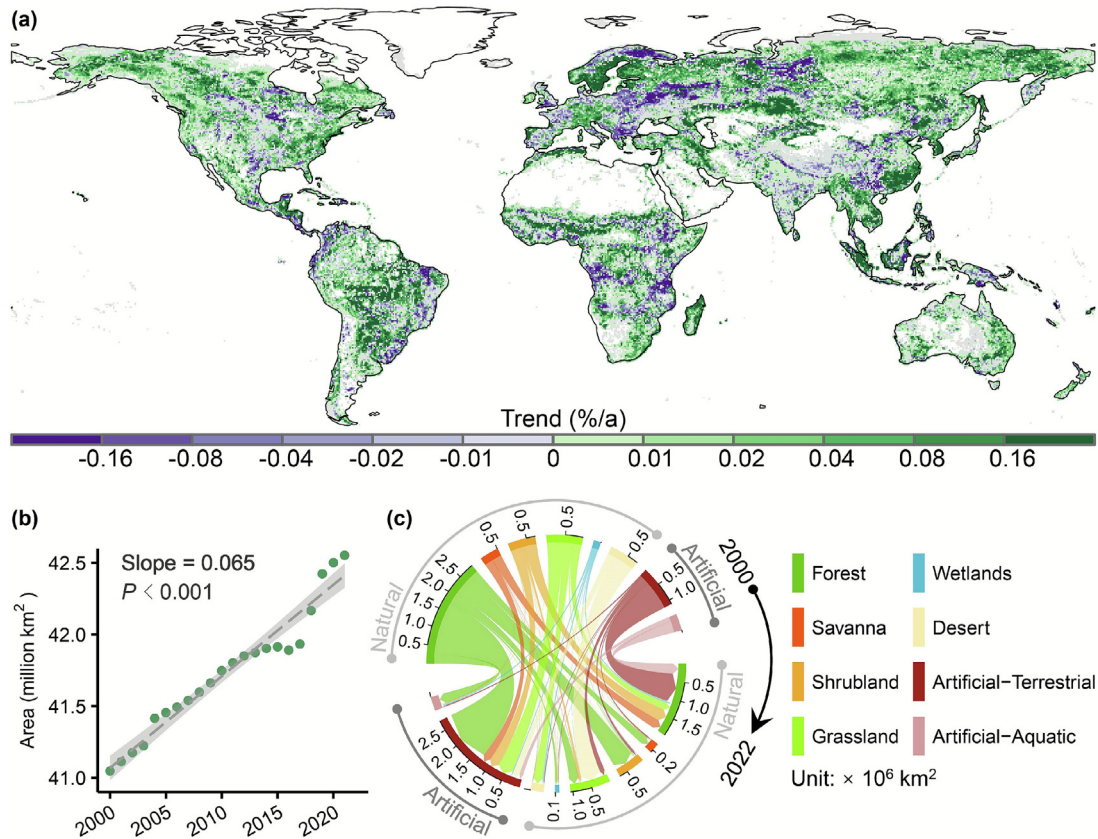
habitat types. We focused on two key questions: (1) How have these habitats shifted over the past two decades? (2) What factors are most strongly associated with these changes?

To answer these questions, we used annually resolved global maps of host bird habitats generated using a decision tree approach [8] that integrates land cover with climate, biome, and elevation layers (Supplementary material). These maps classify eight IUCN-defined habitat types: six natural types (forests, savannas, shrublands, grasslands, wetlands, and deserts) and two artificial types (artificial-terrestrial and artificial-aquatic) (Fig. S1 and Table S1 online), with an accuracy of 0.84. Artificial-terrestrial habitats were mapped using ESA CCI land-cover classes, including rainfed croplands (herbaceous, tree, or shrub cover dominated), cropland-natural vegetation mosaics, and urban areas. Artificial-aquatic habitats were derived from flooded categories, including tree, shrub, or herbaceous cover inundated by fresh, brackish, or saline water (Table S2 online). We quantified long-term trends in the extent of each habitat type and analyzed transition pathways among them, revealing contrasting trajectories of natural habitat loss and artificial habitat expansion (Supplementary material). We then used a machine-learning method to identify the main drivers of these transformations (Supplementary material).

We found strong and contrasting long-term trends in natural and artificial habitats of AIV host bird species, a pattern consistent across 25-km, 50-km, and 100-km grids (Fig. 1a and Figs. S2–S4 online). Artificial habitats expanded significantly, increasing from 41.05 million km<sup>2</sup> in 2000 to 42.62 million km<sup>2</sup> in 2022 (slope = 0.065,  $P < 0.001$ ), with the most rapid increases in South

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**Fig. 1.** Spatiotemporal dynamics and transformation patterns of AIV host bird habitats from 2000 to 2022. (a) Spatial patterns of trends in artificial habitat (artificial-terrestrial and artificial-aquatic) across 50 km × 50 km grid scales. Purple and green denote significant decreasing and increasing trends, respectively ( $P \leq 0.05$ ), while gray indicates non-significant trends. The base map is from the standard map service of the Ministry of Natural Resources of China (<http://bzdt.ch.mnr.gov.cn/>), Map No. GS (2021) 5445. (b) Time series of total artificial habitat area from 2000 to 2022. (c) Global habitat transformation pathways among the eight IUCN-defined habitat types. Colors correspond to the eight habitat categories—forests, savannas, shrublands, grasslands, wetlands, deserts, artificial-terrestrial, and artificial-aquatic—as shown in the legend. In the chord diagram, the upper arcs (arrow origins) depict habitat losses from 2000, and the lower arcs (arrow termini) represent gains by 2022. Arrow width corresponds to the area transformed between habitat types.

Asia, Southeast Asia, Northern Europe, and South America (Fig. 1a, b). In contrast, natural habitats declined substantially over the same period (slope =  $-0.067$ ,  $P < 0.001$ ) (Fig. S2 online). Examination of trends within individual habitat types further clarified these patterns (Fig. S5 online). Among artificial habitats, terrestrial types expanded continuously, whereas aquatic types decreased in the period but rebounded after approximately 2017. Among natural habitats, forests, savannas, wetlands, and deserts all experienced persistent contraction, indicating widespread loss across ecosystems used by host species. Wetland losses are particularly consequential for Anseriformes—the primary natural hosts of AIV—whose strong dependence on wetlands makes them especially vulnerable. Shrublands declined early but partially recovered, resulting in no significant net change. Grasslands were the only natural habitat type to show overall expansion, likely reflecting region-specific land conversions rather than ecological restoration. Together, these findings highlight divergent trajectories of natural and artificial habitats and the growing dominance of human-modified landscapes within AIV host bird habitats.

To evaluate the habitat conversion processes underlying these shifts, we quantified directional transitions among habitat types. The results reveal a pronounced and persistent trend toward artificialization of AIV host bird habitats over the past two decades (Fig. 1c). Between 2000 and 2022, approximately 3.01 million km<sup>2</sup> of natural habitats were converted into artificial types (i.e., habitat artificialization), compared with only 1.42 million km<sup>2</sup> restored from artificial to natural habitats (i.e., habitat restora-

tion)—a more than twofold imbalance that highlights sustained anthropogenic encroachment into natural ecosystems. Forests accounted for the largest share of conversions (1.77 million km<sup>2</sup>), followed by grasslands (0.45 million km<sup>2</sup>), shrublands (0.31 million km<sup>2</sup>), savannas (0.23 million km<sup>2</sup>), deserts (0.19 million km<sup>2</sup>), and wetlands (0.07 million km<sup>2</sup>). In contrast, most restoration originated from artificial-terrestrial habitats (1.08 million km<sup>2</sup>), with smaller gains from artificial-aquatic areas (0.34 million km<sup>2</sup>). These asymmetric transitions indicate a global net shift from natural to artificial habitats, with important implications for AIV host ecology and the intensification of wildlife-human interfaces.

Habitat transformation was pervasive across all major biogeographic realms, although its magnitude varied (Fig. S6 online). The Palearctic realm experienced the largest absolute expansion of artificial habitat (1.39 million km<sup>2</sup>), followed by the Neotropical (0.52 million km<sup>2</sup>), Nearctic (0.39 million km<sup>2</sup>), Afrotropical (0.37 million km<sup>2</sup>), Indomalayan (0.22 million km<sup>2</sup>), and Australian (0.11 million km<sup>2</sup>) realms. In all regions, forest-to-artificial transitions dominated conversion pathways. For example, forest loss accounted for 77.4% and 70.0% of newly formed artificial habitats in the Neotropical and Indomalayan realms, respectively, reflecting extensive encroachment into forested ecosystems. These realm-specific dynamics illustrate both the global scale and regional heterogeneity of habitat artificialization affecting AIV host birds in the 21st century.

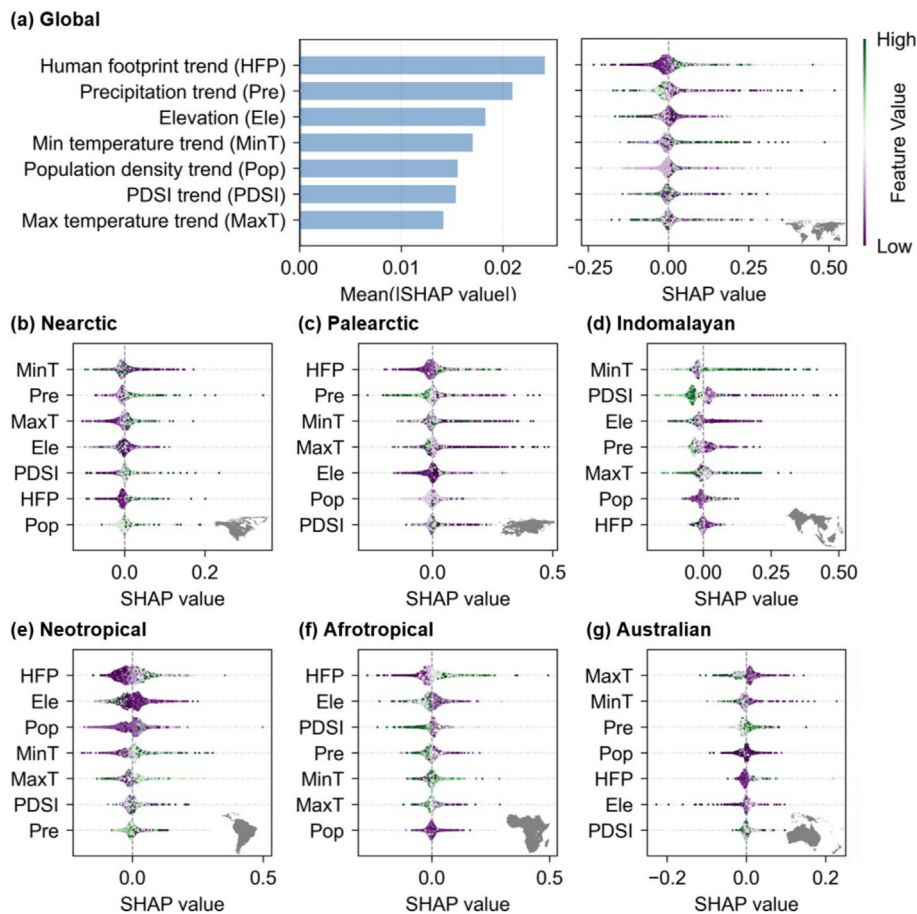
To investigate the drivers of anthropogenic transformation in AIV host bird habitats, we employed Random Forest (RF) models

integrating human, climatic, and environmental predictors, and quantified their contributions using Shapley Additive exPlanations (SHAP) (Supplementary text and Fig. S7 online). At the global scale, the model explained 50.6% of the spatial variance in artificial habitat trends. Model performance varied among realms, with  $R^2$  values of 46.0% in the Nearctic, 57.5% in the Palearctic, 41.0% in the Indomalayan, 44.0% in the Neotropical, 48.8% in the Afrotropical, and 49.6% in the Australian realm. SHAP values were used to assess the marginal importance of individual predictors in each case.

Globally, human-related factors overwhelmingly dominated the expansion of artificial habitats for AIV host bird species (Fig. 2a). The human footprint trend was the strongest predictor, capturing the effects of escalating anthropogenic pressures such as urban growth, expanding infrastructure, and intensifying land use. Many host bird habitats already occur within highly modified landscapes, particularly in East Asia, Southeast Asia, the United States, and Europe (Fig. S8 online). Since 2000, human pressures have intensified in regions including the eastern United States and Southeast Asia, mirroring the pronounced artificialization observed in these areas (Fig. 1a and Fig. S9 online). Population density trends also contributed to habitat expansion, indicating that demographic shifts remain an important correlate of land transformation. Among environmental predictors, elevation exhibited a notable effect: lower-lying areas tended to show positive SHAP values, suggesting greater susceptibility to conversion due to higher accessibility and

development potential. Climate-related variables played a secondary role. Trend in precipitation and the Palmer Drought Severity Index (PDSI) made moderate contributions—wetter or less drought-prone regions were more likely to experience artificial expansion, potentially reflecting improved agricultural viability or greater infrastructure resilience. By contrast, temperature trends (mean, minimum, and maximum) ranked lowest, indicating a limited influence on the spatial distribution of habitat expansion during the study period.

The dominant drivers of habitat artificialization varied across biogeographic realms (Fig. 2b–g). In the Afrotropical, Neotropical, and Palearctic realms, the human footprint consistently emerged as the strongest predictor, underscoring the pervasive influence of anthropogenic expansion in these regions (Fig. 2c, e, and f). In contrast, climate-related variables—particularly long-term trends in precipitation and temperature—play a more prominent role in the Australian, Nearctic, and Indomalayan realms (Fig. 2b, d, and g), indicating that habitat transformation there is more tightly constrained by biophysical conditions. This spatial heterogeneity highlights the importance of regional context in shaping the dynamics of AIV host bird habitats. Although human pressures dominate at the global scale, their influence is modulated by local climatic and environmental settings. Effective conservation and land-use strategies will therefore need to integrate both anthropogenic and ecological drivers to mitigate habitat loss and its potential zoonotic implications.



**Fig. 2.** Explanatory power of multiple factors in anthropogenic transformation of AIV host bird habitats. (a) Global feature importance and SHAP value distributions for predictors of artificial habitat trends. (b–g) SHAP summary plots showing predictor effects across the six biogeographic realms: Nearctic (b), Palearctic (c), Indomalayan (d), Neotropical (e), Afrotropical (f), and Australian (g). Each point represents the SHAP value for a single grid cell, with colors indicating the corresponding predictor value (purple: low, green: high). Predictors include human footprint trend (HFP), precipitation trend (Pre), elevation (Ele), PDSI trend (PDSI), population density trend (Pop), and temperature trends (MinT, MaxT). Insets in each panel delineate the geographic extent of the corresponding biogeographic realm.



Our results reveal an extensive anthropogenic transformation of AIV host bird habitats over the past two decades, driven primarily by the conversion of forest and other natural ecosystems (Fig. 1 and Figs. S2–S5 online). This trend was most pronounced in biodiversity-rich regions such as Southeast Asia and South America, where agricultural expansion and urbanization have accelerated in recent decades [9]. RF models identified human footprint trends as the principal driver of habitat artificialization (Fig. 2), consistent with global evidence demonstrating the central role of human activity in shaping land-use change [10]. The human footprint encompasses pressures highly relevant to AIV host bird habitats and potential spillover interfaces. Agricultural expansion, for example, increases contact between wild waterbirds and poultry in rice paddies and irrigated landscapes; urban and peri-urban growth creates shared environments for wild birds, domestic animals, and humans; and infrastructure networks, including roads and railways, fragment habitats while facilitating human access. These mechanisms help explain why human footprint aligns closely with ecological contexts that promote cross-species contact and potential viral transmission.

Environmental factors also modulated the spatial patterns of transformation. Artificial habitats were more likely to emerge in low-lying, accessible landscapes conducive to infrastructure development [11]. Regions experiencing increased precipitation or reduced drought stress were likewise more prone to artificial expansion [12,13], likely reflecting enhancements in agricultural viability or the resilience of built environments. Together, these findings underscore the interplay between human pressures and environmental context in shaping habitat transformation, particularly in densely populated, biodiversity-rich regions. By leveraging globally consistent, annually resolved habitat maps for AIV host birds, this study provides a robust characterization of the spatiotemporal patterns and primary drivers of habitat change, thereby advancing the ecological understanding of how anthropogenic and environmental forces are reshaping the landscapes available to these species.

The expansion of artificial habitats has important implications for wildlife-domestic animal interfaces and potential AIV spillover. Over the past two decades, artificial landscapes have expanded markedly, bringing wild birds into closer proximity with human-dominated environments. Anthropogenic landscapes—such as rice paddies, irrigated areas, and peri-urban areas—are well-established convergence zones for waterbirds, domestic poultry, and humans [14], thereby creating opportunities for cross-species viral transmission. Our results suggest that these interfaces are intensifying, particularly in rapidly developing regions such as Southeast Asia and South America, where habitat change has been most extensive. Artificial habitats may also provide novel or supplemental food resources (e.g., crops [15]), potentially altering movement ecology and promoting local aggregation of AIV host species. These shifts, combined with ecological degradation or fragmentation of transformed habitats, may reduce suitability for some species while concentrating others in suboptimal environments, thereby reshaping ecological interactions and potentially heightening spillover risks.

Although this study focuses on habitat change rather than viral dynamics, the findings offer essential spatial context for future research and management. Integrating habitat trends with avian movement tracking, AIV surveillance, and social-ecological indicators will be critical for identifying high-risk landscapes. Artificialization hotspots that coincide with host diversity-rich and densely populated regions—such as Southeast Asia and South America—emerge as priority areas where conservation, land-use planning, and One Health interventions should be jointly implemented. Policy priorities include embedding habitat conservation within agricultural development strategies, strengthening biosecurity

at farm and peri-urban interfaces, and establishing coordinated wildlife-poultry-human surveillance systems. Targeting resources toward such high-risk environments offers an effective pathway for mitigating potential zoonotic spillover under the One Health framework.

In summary, this study documents a substantial global shift in the terrestrial habitats of AIV host birds from 2000 to 2022, characterized by the expansion of artificial habitats at the expense of natural ecosystems—particularly forests. This transformation is most pronounced in biodiversity-rich regions such as Southeast Asia, South America, and central Sub-Saharan Africa, where human pressures strongly shape habitat trajectories. By revealing how anthropogenic and environmental drivers interact to redefine the ecological space of AIV host birds, our study provides a critical baseline for anticipating where wildlife-poultry-human interfaces are intensifying. This ecological foundation can guide conservation priorities, inform land-use policy, and support One Health strategies aimed at reducing the risk of future zoonotic emergence.

### Conflict of interest

The authors declare that they have no conflict of interest.

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### Author contributions

Keping Ma, Jinwei Dong, Qiang Zhang, and Zhichao Li conceptualized and designed the study. Qiang Zhang conducted all the analysis and drafted the initial manuscript. All authors contributed to the interpretation of results and the revision of the manuscript.

### Data availability

The scripts are freely available at <https://github.com/QiangHHZ/BirdHabitatChange>.

### Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scib.2025.12.035>.

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