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Ecology

Birds migrate longitudinally in response to the resultant Asian monsoons of the Qinghai-Tibet Plateau uplift

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eLife Assessment

This **important** and creative study finds that the uplift of the Qinghai-Tibet Plateau-via its resultant monsoon system rather than solely its high elevation-has shifted avian migratory directions from a latitudinal to a longitudinal orientation. However, the main claims are **incomplete** and only partially supported, as the reliance on eBird data-which lacks the resolution to capture population-specific teleconnections-combined with a limited tracking dataset covering only seven species leaves key aspects of the argument underdetermined, and the critical assumption of niche conservatism is not sufficiently foregrounded in the manuscript. More clearly communicating these limitations would significantly enhance the interpretability of the results, ensuring that the major conclusions are presented in the context of these essential caveats.

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Abstract

The uplift of the Qinghai-Tibet Plateau is one of the greatest geological events on Earth, pivotally shaping biogeographic patterns across continents, especially for migratory species that need to overcome topographical barriers to fulfil their annual circle. However, how the uplift influences animal migration strategies remains largely unclear. We compare the current flyways of 50 avian species migrating across the plateau with those reconstructed before the uplift as a counterfactual. We find that the major effect of the plateau uplift is changing avian migratory directions from the latitudinal to the longitudinal. The monsoon system generated by the uplift rather than the high elevation *per se* shapes those changes. These findings unveil how an important global geological event has influenced biogeographic patterns of migratory birds, yielding testable hypotheses for how observed avian distributions emerge.

Introduction

The Qinghai-Tibet Plateau (QTP) is the most extensively elevated surface on Earth, with an average elevation of ~5 km over an area of 2.5 million km^2 [1]. The uplift of the plateau exerts profound influences on the environment and determines the biogeographic boundaries both within and across continents [2]. The unique geological developments of the QTP, especially its high elevation, are believed to have influenced various taxonomic groups continuously [3–5]. However, the plateau's uplift also brings up Asian monsoons, one of the most vigorous phenomena in the global climate system [6,7]. The Asian monsoons dominate large areas extending from the Indian sub-continent eastwards to Southeast and East Asia [8]. Their evolution and variability have caused significant variations in the redistribution of water and heat via a series of natural processes, such as drought, flood, and heat waves [6]. Given the large impacts of Asian monsoons on climate and environments, they can reconfigure the spatial patterns of biodiversity and ecosystem processes. This entails movement patterns that shape the effects of the environment on organisms [9–11]. However, owing to the difficulties in studying the complex effects caused by monsoons, most studies that explored the influence of the QTP just conceived the plateau as an orographic barrier [12–14]. The role of monsoons in shaping species movement patterns remains poorly understood.

Animal movement underpins species' spatial distributions and ecosystem processes. An important animal movement behaviour is migrating between breeding and wintering grounds [15–17]. Those migratory journeys have intrigued a body of different approaches and indicators to describe and model migration, including migratory direction, speed, timing, distance, and staging periods [18,19]. Amongst them, the migratory direction is one of the most prominent indicators for migration patterns, evidenced by a majority of animals migrating latitudinally between wintering and breeding areas [20]. This can be explained by not only the fact that wintering sites are usually located in the warmer south (e.g. tropic) and breeding sites located in the cooler north (e.g. arctic), but also the earth's magnetic fields that are arguably believed to affect the latitudinal migration of animals [21–24]. However, the migratory direction can be changed from latitudinal to longitudinal when the animal faces environmental changes [20,25–28].

Environmental fluctuations in the QTP are relatively small over the *longue durée* after the final-stage uplift [29], but few studies have evaluated how environmental heterogeneity across the QTP might influence the migratory behaviour of birds (but see migratory pattern descriptions, e.g., Zhao et al. [30], Pu and Guo [31]). Yet it remains unclear whether and how these shifts systematically alter species' migration patterns rather than a simple assumption that the QTP birds exploit resources according to their availability. Therefore, testing whether migration patterns vary consistently for birds that migrate across the QTP is key to our understanding of the processes that determine movement patterns and provides insights into how they may affect community organisation and functioning under the context of global environmental change.

In this work, we leverage the community-contributed and satellite-tracking data to explore the impacts of the QTP uplift in terms of both the development of its high elevation and Asian monsoons on the migratory strategies for the birds that migrated across the plateau. We do this by reconstructing the environments before the uplift and contrasting migratory directions of 50 bird species (See Table S1 for a full list of species) between breeding and wintering areas in environments before the uplift with those at present. Thus, the simulated environments before the uplift of the plateau serve as a counterfactual state. Counterfactual is an important concept to support causation claims by comparing what happened to what would have happened in a hypothetical situation: “If event X had not occurred, event Y would not have occurred” [32]. Recent years have seen an increasing application of the counterfactual approach to detect biodiversity change, i.e., comparing diversity between the counterfactual state and real estimates to attribute the factors causing such changes e.g., Gonzalez et al. [33]. Whilst we do not aim to provide causal inferences for avian distributional change, using the counterfactual approach, we are able to estimate the influence of the plateau uplift by detecting the changes of avian distributions, i.e., by comparing where the birds would have distributed without the plateau to where they currently distributed. We regard the counterfactual environments as an ideal tool for eliminating, to the extent possible, vagueness, as opposed to simply description of current distributions of birds.

We also calculate the migratory directions (azimuths) between adjacent stopover sites, breeding and wintering areas *en route*, and assess the relationship between migratory directions and environmental stress. Our findings yield the most comprehensive picture to date of how the QTP uplift shapes migratory patterns of birds, revealing insights into the challenges and opportunities for migratory birds in a changing world.

Results and discussion

We have two major findings regarding distribution patterns and migratory directions of QTP birds. First, we developed a dynamic species distribution modelling [18] to track the weekly distribution of target species, capturing the interconnections of stopover, wintering and breeding areas (See methods for details). By contrasting their distributions before and after the uplift, we find the distribution of migratory birds extended in longitude and narrowed in latitude with the uplift of QTP (**Figure 1-E**, G, and I). Birds are more likely to migrate along a longitudinal gradient in present environments as a result of the QTP uplift (See Table S1 for AUC values for model performance of each species). Specifically, before the uplift, migratory birds have a higher probability of breeding across a vast area at low and middle latitudes on the Eurasia continent, including West Asia, Siberia, QTP regions, and even Africa, whilst their most likely breeding areas move northeastward to the extreme north of Russia after the uplift. Different from the breeding area, the wintering area of migratory birds has a larger change in distribution probability. Birds that migrate across the QTP in the modern scenario have a higher probability of wintering in Southwest Asia and North Africa, whereas they have a higher probability of moving southeast to winter in Southern China and more areas of Africa before the uplift (**Figure 1-D F** and **H**)..

Second, our results show that wind cost, temperature, and precipitation are three major factors that influence the overall migratory directions (both autumn and spring) of birds, despite the differences in autumn and spring migration across different geographic areas (**Figure 2**). During autumn migration, wind cost is the most important factor for birds’ migration direction (**Figure 2**). A higher wind cost is associated with migration, which suggests a higher opportunity for birds to use the wind to facilitate their longitudinal migration (Figures S1 and S9). They also choose to follow a flyway of relatively higher annual precipitation and temperature as they migrate from breeding areas to wintering areas during autumn migration (Figure S2, S3 and S9). Apart from those three factors, no evidence is found for strong impacts of elevation and vegetation on the direction of migration (**Figure 2** and Figure S9).

Aside from the broad influences of QTP uplift, when migrating across different geographic areas, i.e., areas west of (longitude < 73°E, West QTP), areas in the central (73°E ≤ longitude < 105°E, middle QTP), and areas east of the QTP (longitude ≥ 105°E, East QTP), birds diversify their preferences in environmental conditions. Despite the fact that wind cost is the most important factor for the overall autumn migration, temperature is the most prominent factor in the areas east of the QTP and in the central QTP (**Figure 2** and Figure S9). In addition, the average annual temperature in the central QTP is lower than that in the areas east of the QTP, but birds migrate

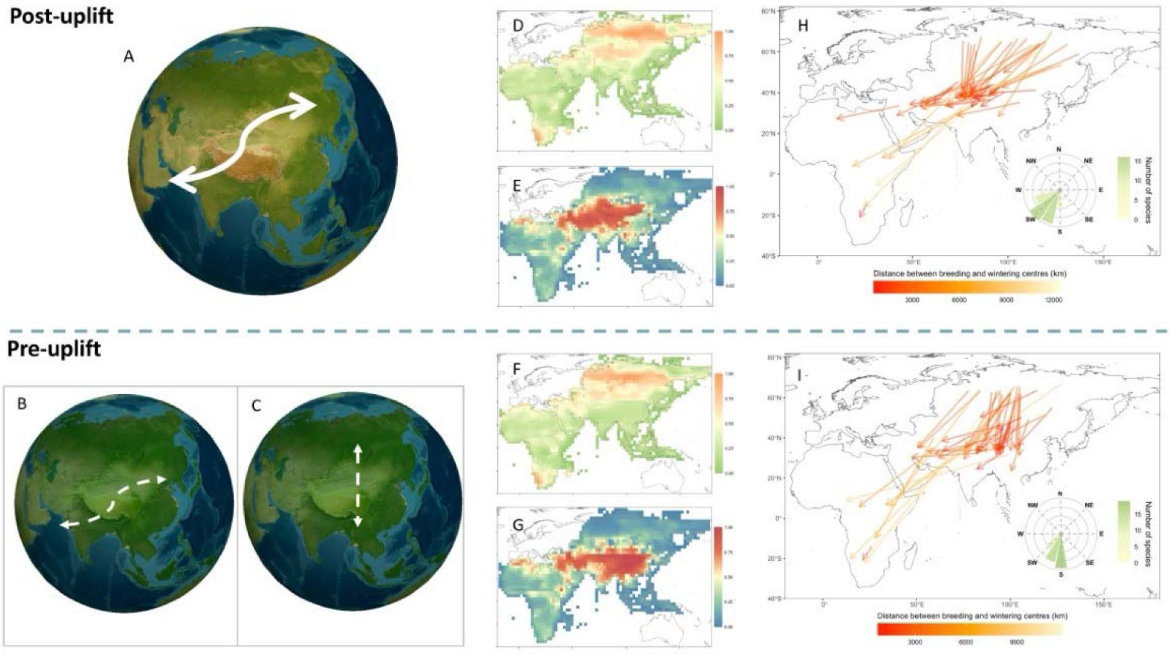

Figure 1.

Influence of the Qinghai-Tibet uplift on avian migration strategies.

(A) – (C) Schematic example of the role of Qinghai-Tibet Plateau (QTP) uplift in distribution patterns of migratory birds. **(A)** Birds migrate with a large longitudinal range in modern environments. Before the QTP uplift, birds may maintain similar migratory patterns with large longitudinal changes **(B)** or migrate with few longitudinal changes between wintering and breeding areas **(C).** The occurrence probability of 50 migratory bird species under modern environments in breeding areas **(D)** and wintering areas (**E**). The occurrence probability of birds in breeding areas **(F)** and wintering areas (**G**) before the QTP uplift. Migratory directions are identified at present (**H**) and before the uplift (**I**). The direction and length of the arrow represent migratory direction (measured by the azimuth angle) and distance from centres of breeding to wintering areas for each species. The circular barplot of the inset panel denotes the summary of migratory directions from breeding to wintering areas for each bird species, where the height and colour of the bars represent the number of species.

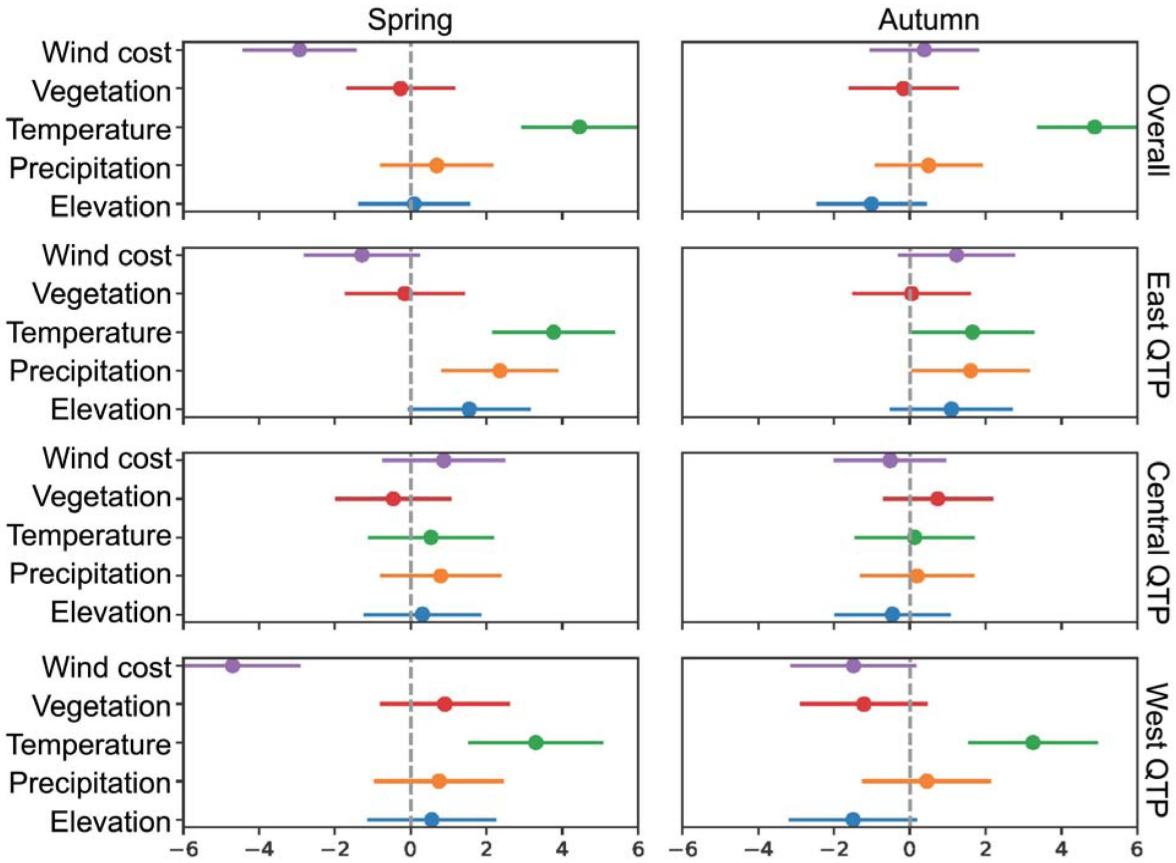

Figure 2.

The influence of environmental factors on the direction of avian migration.

Migratory directions are calculated based on the azimuths between each adjacent stopover, breeding and wintering areas for each species. We employ multivariate linear regression models under the Bayesian framework to measure the correlation between environmental factors and avian migratory directions. Wind represents the wind cost calculated by wind connectivity. Vegetation is measured by the proportion of average vegetation cover in each pixel (~1.9° in latitude by 2.5° in longitude). Temperature is the average annual temperature. Precipitation is the average yearly precipitation. All environmental layers are obtained using the Community Earth System Model. West QTP, central QTP, and East QTP denote areas in the areas west (longitude < 73°E), central (73°E ≤ longitude < 105°E), and east of (longitude ≥ 105°E) the Qinghai-Tibet Plateau, respectively.

across those two areas with increasing temperatures consistently (Figure S2, S6 and S9). Once they reach the regions west of the plateau (West QTP), low wind cost in the longitudinal direction and higher precipitation become priority choices for their migration (**Figure 2** and Figure S9).

Compared with autumn migration, higher temperatures act as a major clue in the areas east and west of the plateau during spring migration, whereas the westerly outweighs temperature when birds migrate in the central plateau (**Figure 1**, Figure S1, S3 and S9). Besides temperature, precipitation also plays a role in all stages of spring migration. When birds migrate, they tend to follow a flyway of decreasing annual precipitation. Elevation has a slightly larger impact at the early stages of migration, i.e., areas east of the plateau during autumn migration and areas west of the plateau during spring migration, as birds migrate towards higher elevations during these stages.

It is commonly claimed that the initiation of migration is inherently inflexible in migratory birds [34], owing to the weak or insufficient responses by migratory birds to adjusting migration behaviour (e.g., migration timing and route) [35]. This claim is particularly invoked for long-distance migrants, who may face greater temporal (e.g., migration timing) or physiological constraints given the varied phenologies *en route* [35]. Our results show that a major change in avian migratory patterns in response to environmental change can be adjusting migration direction from the latitudinal to the longitudinal at the scale of their whole migration circle. This highlights substantial changes in migratory bird distribution and their biogeographic patterns as a result of the uplift of the Qinghai-Tibet Plateau (**Figure 1**).

One of the biggest climatic consequences of the uplift of the Qinghai-Tibet Plateau is the development of a unique monsoon system that has shaped environments across continents [36]. One typical feature of Asian monsoons is the seasonal climatic change, comprising a dry cold winter phase and a wet warm summer phase [36]. Asian monsoons also consist of several sub-systems, including the northeast monsoon and the East Asian winter monsoons that dominate the weather and climate in different parts of the plateau across different geographical periods. Our results showed that wind cost, temperature, and precipitation have more important impacts on avian migration than elevations in different geographic areas (**Figure 2**). This suggests that the monsoon system, rather than the high elevations of the plateau *per se*, is an important factor during avian migration on the plateau (**Figure 2**). Specifically, when birds begin their autumn migration in early September, the influence of the Siberian High on migration emerges as the East Asian winter monsoons start to reach the area east of the QTP, and their impacts at this stage are mainly reflected by varied temperatures and relatively less precipitation [37,38]. This can explain why higher temperatures and more precipitation play a more important role than wind cost in the area east of the plateau (**Figure 2**) since higher annual temperatures and more precipitations mean more food resources for migrants [39,40], whereas wind during this period is less strong than that in winter [38]. Whilst birds migrate westwards, less wind cost is becoming more important to determine their migration direction. This is, on the one hand, because the northeast monsoon begins to dominate the climate in the southwest of the QTP from around the end of September [41]. The northeast monsoon brings cold wind to sweep the Qinghai-Tibet Plateau down towards the vast spans of the Indian Ocean [41], which could facilitate the westward migration of birds. On the other hand, in the northwest of the Qinghai-Tibet Plateau, the extended Siberia High and associated atmospheric systems that deliver cold and dry air masses to the Mediterranean surface also provide positive wind conditions for migrants [42].

When migrating toward breeding grounds in spring, birds adopt strategies different from their autumn migration, accompanied by different effects of environment on their migratory directions. Temperature becomes more important than wind cost in spring migration (**Figure 2** and S9). Given high temperatures usually mean relatively rich food resources for birds [43,44], this suggests that birds that migrate across the Qinghai-Tibet Plateau may focus on energy accumulation during their spring migration rather than reducing flight costs in an effort to meet the energetic demands. Those birds also tend to follow a more ‘capital’ breeding strategy where birds rely on endogenous reserved energy gained prior to reproduction [45] rather than an ‘income’ breeding strategy where birds ingest nutrients mainly collected during the period of reproductive activity [46]. This collaborates with studies on breeding strategies of migratory birds in Asian flyways [47]. Another important reflection of the migration strategy is the role of elevation during different geographic areas of migration. As the elevation in the areas east and west of the plateau is much lower than that in the central, when migratory birds fly across the plateau, they need to follow a turned “u-shaped” elevation distribution and fly toward a higher elevation at the early and late stages of spring migration. This also implies that more energy is needed at the beginning of spring migration. Considering the need to balance energy accumulation and flight cost, areas with higher annual average temperatures and precipitation with high-level food resources are preferred during this migration stage to meet birds’ energy requests.

Caveats and conclusions

Whilst we adopted both community-contributed and tracking data where potential biases existed, there are caveats to be aware of when interpreting our results. First, we used adaptive spatiotemporal modelling to address the imbalanced distribution of sampling in eBird data, but more sampling efforts and observations are still needed in areas of sparse records to better model and predict changes of species distributions. Second, tracking data can provide detailed information of the movement patterns of species but are limited to small numbers of species due to the considerable costs and time needed. We aimed to adopt the tracking data to examine the influence of focal factors on avian migration patterns, but only seven species, to the best of our ability, were acquired. Similar results were found in studies that used tracking data to estimate the distribution of breeding and wintering areas of birds in the plateau [e.g., 30,31,48-54]. The results based on seven species are rigour, but their implications could be restricted by the number of tracking species we obtained. We call for more tracking data to test and investigate the influence of QTP on multiple aspects of avian migratory patterns.

Despite these caveats, our study provides a novel understanding of how QTP shapes migration patterns of birds. Albeit with the extensive influence of the plateau uplift on geology and geography, the resultant monsoon system, rather than its high elevation, is found to be a key factor shaping present avian migration patterns. Our study unveils shifts in avian migratory directions and their underlying mechanisms in the contexts of the QTP uplift, enhancing comprehension of the complex biogeographic effects on animal migration.

Methods and materials

Summary

We used two approaches to determine the migratory flyways of birds across the Qinghai-Tibet Plateau. First, we quantified the distributional change of each avian species by comparing the distribution range before and after the uplift of the plateau. For the present distribution, we used a dynamic spatiotemporal abundance model - Adaptive Spatiotemporal Model (AdaSTEM) that we have developed - to obtain the seasonal distribution of birds [18]. We then used a species distribution model (i.e., MaxEnt) to measure the correlation between present distribution and environments [55]. We calculated the distribution of migratory birds before the uplift of the plateau by projecting the correlation between their current distribution and environments onto environments before the uplift. Second, we obtained the specific migratory routes for each species by measuring the migratory directions (i.e., the azimuth angle between adjacent stopover sites and breeding and wintering areas) *en route*. Similarly, we used the relationships between present migratory directions and environments to predict the migratory directions pre-uplift of the plateau. Since our aim here was a prediction, we used random forest models, but we also used Bayesian multivariate regression modelling to measure the influence of environments on migratory directions of birds.

eBird checklist

We used a community-contributed database for the dynamic spatiotemporal abundance model to measure the seasonal distribution. Specifically, we first obtained the list of bird species that might migrate across the Qinghai-Tibet plateau based on Prins and Namgail [56]. We then requested and downloaded the eBird Basic Dataset in Feb 2022 [57] for 64 species. We then excluded species that were not listed as "full migrant" in BirdLife International (*https://datazone.birdlife.org*), which resulted in a total of 50 avian species analysed in our study and covered breeding populations in geographical Asia. We used data from the year 2019 to avoid the potential influence of the pandemic on bird observation [58,59] and bird behaviour [60].

The eBird data may be biased by the imbalanced sampling and variation of observers' skills in identifying species. To address spatiotemporal imbalances in data distribution and the potential overrepresentation of birding hotspots, we conducted spatiotemporal subsampling following the method proposed [61,62]. We first assigned each checklist with a global hexagonal hierarchical geospatial indexing system [H3 system; 63,64], with a resolution of level 7 (~5.16 km per cell). Then, to avoid biased sampling in rare species with unusual active temporal periods, we split the 24 hours of the day into 12 equal bins and assigned a checklist to each of the bins. We then randomly subsampled only one checklist for each year - day of the year - hour bin of day - cell combination. The subsampling resulted in 5,037,088 checklists for the year 2019.

To account for difference of observers' expertise in recognising species,, we calculated the historical cumulative species count for each bird observer throughout their historical eBird checklists prior to 2019 as a proxy to measure the expertise of bird observers [65]. We then filtered the checklists as suggested by recent studies [61,62]:

1. Only checklists labelled as complete were included.
2. Only checklists with Traveling or Stationary protocol types were included. For checklists with the protocol type Traveling, only those with a travelling distance of less than 3km were included.
3. The observation duration should be longer than 5 min and shorter than 300 min.
4. Observers with expertise lower than 2.5% percentile were removed since they are less representative and may induce large bias.

Predictor variables for spatiotemporal abundance modelling

For each remaining checklist, we extracted six types of environmental variables based on their geographical coordinates:

1. Sampling effort variables, which include protocol type, travelling distance, observation duration minutes, number of observers, and observers' expertise (measured in historical species count).
2. Temporal variables, which include day of year and observation started time of day.
3. Topographic variables, which include the mean and standard deviation of elevation, slope, north, and east aggregated within the 3 km × 3 km buffered area for each checklist. The Topographic data was downloaded from EarthEnv [66] in a 1 km resolution.

4. Land cover data. We used the Copernicus Climate Change Service (C3S) Global Land Cover data with a 300 m resolution [67]. We calculated the landscape variables for each of the land cover types presented in the 3 km × 3 km buffered area for each checklist, including percentage cover, patch density, largest patch index, edge density, mean patch size, standard deviation of patch size for each land cover type, and entropy across heterogeneous land cover patches.
5. Bioclimate variables. We downloaded the ERA-5 hourly data at a 0.25° resolution [68]. Hourly data of a 2 m temperature and total precipitation layer were firstly aggregated to daily level by taking the average. The day-level data were calculated using 19 bioclimate variables, which were then assigned to each checklist according to the geographical coordinates.
6. Normalized Difference Vegetation Index (NDVI). NDVI data were extracted from Terra Moderate Resolution Imaging Spectroradiometer (MODIS) Vegetation Indices 16-Day (MOD13A2) Version 6.1 product with a resolution of 16 days and 1 km [69]. We further aggregated the data to hexagon level 5 based on the H3 indexing system (with edge length ~9.85km). For each hexagon, we leveraged the pyGAM package [70] to apply a GAM model with 30 splines to interpolate the data to temporal ranges that were not provided by the original data. This resulted in a daily resolution dataset. We calculated six features based on NDVI and included them in subsequent modelling, i.e., the median, maximum, and minimum of NDVI, and the median, maximum, and minimum of the first derivative of NDVI against day of year (sometimes referred to “green wave”) for each hexagon throughout the year.

The feature engineering resulted in 106 predictor variables, including 6 sampling effort variables, 2 temporal variables, 8 topographic variables, 19 annual climatic variables, 65 land cover variables, and 6 vegetation index-related variables. All calculations are conducted in Python version 3.9.0.

Spatiotemporal abundance modelling

To adjust for sampling error and obtain the general migration pattern incorporating interconnections of stopover, wintering and breeding areas across species, we applied an Adaptive Spatio-Temporal Model (AdaSTEM) for each species to model weekly distributions of birds using stemflow package version 1.0.9.1, which we have recently reported [18].

AdaSTEM is a machine learning modelling framework that takes space, time, and sample size into consideration at different scales. It has been frequently used in modelling eBird data [62,71,72] and has been proven to be efficient and advanced in multi-scale spatiotemporal data modelling. To briefly summarise the methodology, in the training procedure, the model recursively splits the input training data into smaller spatiotemporal grids (stixels) using the QuadTree algorithm [73]. For each of the stixels, we trained a base model only using data contained by itself. Stixels were then aggregated and constituted an ensemble. In the prediction phase, stemflow queries stixels for the input data according to their spatial and temporal indexes, followed by the prediction of corresponding base models. Finally, we aggregated prediction results across ensembles to generate robust estimations (see Fink et al., 2013 [71] and stemflow documentation [18] for details).

We used XGBoost [74] as our classifier and regressor base model for its capability and balance between performance and computational efficiency. We set 10 ensemble folds, a maximum grid length threshold of 25 degrees, a minimum grid length threshold of 5 degrees, a temporal sliding window size of 50 DOY and a step of 20 DOY, and required at least 50 checklists for each stixel in model training. Trained models were then used to predict on prediction dataset with 0.1° spatial resolution and weekly temporal resolution, where the variables were annotated with the same methodology as that of the training dataset. Only spatiotemporal points with more than seven ensembles covered are predicted. In downstream analyses, we removed data points with abundance lower than 0.1 quantiles to obtain reliable predictions for each week.

Environmental variables for species distribution modelling

Given the challenges in simulating environmental and climatic conditions before the uplift of the Qinghai-Tibet Plateau, we modelled the environments before and after the uplift with five variables, i.e., monthly wind (speed and direction), annual temperature, annual precipitation, elevation and annual vegetation.

In detail, following Zhang *et al.* [7], we used version 1.0.4 of the Community Earth System Model (CESM) coupled model with a dynamic atmosphere (CAM4), land (CLM4), ocean (POP2), and sea-ice (CICE4) components to simulate pre-uplift environments. CESM and its previous versions have been widely used in climate modelling, e.g., Meehl et al. [75] and are claimed to be capable of broadly reproducing the features of present-day climate [76]. For CAM4, there is a horizontal resolution of ~1.9° in latitude by 2.5° in longitude and 26 layers in the vertical direction. POP2 adopts a finer grid and has a nominal 1° horizontal resolution (320 × 384 grid points, latitude by longitude) and 60 layers in the vertical direction. The land and sea-ice components share the same horizontal grids as the atmosphere and ocean components, respectively. In CLM4, multiple land surface types and plant functional types (PFTs) are contained within one grid, and CLM4 can be run in a dynamic vegetation mode to simulate natural vegetation, including trees, grass, and shrub plant functional types, e.g., Yu et al. [77] Qiu and Liu [78].

We initiated the modelling with two different scenarios, i.e., the actual elevation and a maximum elevation of 300m. We then used the same default preindustrial simulation for the two scenarios with a modern ice sheet, an atmospheric CO2 concentration of 280 ppmv, modern orbital parameters (the year 1950), modern solar constant (1,365 W/m^2), other atmospheric greenhouse gas concentrations set to preindustrial values (CH4 and N2O set to 760 and 270 ppbv, respectively), and preindustrial aerosol conditions. We ran for 750 model years to ensure the combined atmospheric, ocean, and vegetation effects in response to the uplift of the plateau can be investigated.

Species distribution modelling

We used Maximum entropy (MaxEnt) models to compare the avian distributional change between pre- and post-uplift environments under the assumption that species tend to keep their ancestral ecological traits over time (i.e., niche conservatism). This indicates a high probability for species to distribute in similar environments wherever suitable. Particularly, considering birds are more likely to be influenced by food resources and vegetation distributions [79–81], and the available food and vegetation before the uplift can provide suitable habitats for birds [82], we believe the findings can provide valuable insights into the influence of the plateau rise on avian migratory patterns. Having said that, we acknowledge other factors, e.g., carbon dioxide concentrations [83], can influence the simulations of environments and our prediction of avian distribution. MaxEnt compares the environmental features at presence points to those of pseudo absences to discriminate the suitable area [84]. MaxEnt builds models using a generative approach and thus has an inherent advantage over a discriminative approach, especially when the amount of training data is small [84]. Due to its good performance compared to other species distribution modelling techniques, MaxEnt is widely used in the study of biogeography and conservation biology.

We ran the MaxEnt model using default settings but with 1,000 iterations. For each model, we ran 20 bootstrap replications, and each time 75% of locations were selected at random as training samples, while the remaining 25% were used as validation samples. We applied Area Under the Curve (AUC) of the Receiver Operator Characteristic (ROC)assess the performances of the models

(Table S1). AUC is a threshold-independent measurement for discrimination ability between presence and random points [84]. When the AUC value is higher than 0.75, the model was considered to be good [85,86].

Migratory direction

To obtain the species list of birds that migrate across the Qinghai-Tibet Plateau with available tracking data, we checked Movebank (*movebank.org*) together with literature reporting avian migratory routes across the plateau. For those who did not upload their data to Movebank, we digitalised the routes. Specifically, we built a new geographic layer with the same coordinate systems of each reported route and matched the layer with the images of routes. We then delineate migratory routes on the new geographic layer where the geographic information of the routes was achieved. This resulted in seven representative species that migrated across the plateau.

We used the same environmental variables, except for wind, for the species distribution model to investigate the potential influence of environments on migratory directions. We calculated wind connectivity to account for the influence of wind, considering wind connectivity has been identified as a key factor driving avian flying patterns [87]. Since we aimed to investigate the migration patterns at large spatiotemporal scales, we measured the wind connectivity at a monthly resolution to enable analysis of seasonal differences. We adjusted the R package rWind for the computation. In detail, we replaced the default wind data from the Global Forecasting System atmospheric model with our monthly wind data from CESM as input. For both wind costs before and after the uplift of the plateau, we then calculate the movement cost from any starting cell to one of its eight neighbouring cells (Moore neighbourhood). This includes three parameters, i.e., wind speed at the starting cell, wind direction at the starting cell (azimuth), and the position of the target cell. A movement connectivity map was then determined after performing the default algorithms [88]. We reversed the values of cells on the connectivity map, as we aimed to investigate the influence of wind cost, whereas the map showed the importance of the cell to maintain connectivity.

We used a random forest model and a multivariate linear regression model under the Bayesian framework to analyse the influence of environments on avian migratory directions. We first used the random forest model to measure the correlation between migratory directions and modern environments and predict the migratory direction before the uplift of the plateau. We then compared the influence between modern environments and environments before the uplift using a multivariate linear regression model under the Bayesian framework. We adopted two strategies for those two modelling approaches. First, we applied regression to different combinations of season-stage separately (seasons: spring, autumn; stages: overall, east QTP, central QTP, west QTP), resulting in eight regression models. Second, we additionally included species as random variables by applying hierarchical modelling, which also resulted in eight regression models.

All variables were standardised for comparison. All Bayesian models were conducted with PyMC version 5.5 [89] in Python version 3.9.0 environment. We used a NUTS sampler with a numpyro backend (jax.sample_numpyro_nuts) to run four chains, each with 30,00 tuning and 3,000 posterior chain sampling. We assessed the model convergence using potential scale reduction factor (Rhat) and effective sample size (ESS), where all parameters in all models met the criteria of Rhat < 1.03 and ESS > 400.

Additional information

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Author contributions

XZ, WZ, and ZG conceived the idea and designed the methodology of the study, WZ, ZG, YC and ZR performed the analyses and XZ shaped the study. WZ and XZ wrote the paper. All authors contributed critically to the drafts and gave final approval for publication.

Data and materials availability

All data, code, and materials used in the analysis are available from GitHub (*https://github.com/plmyann/QTPbirds*).

Additional files

Supplemental Figures S1-S9 and Table S1.

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Reviewer #1 (Public review):

Strengths:

This is an interesting topic and a novel theme. The visualisations and presentation are to a very high standard. The Introduction is very well-written and introduces the main concepts well, with a clear logical structure and good use of the literature. The Methods are detailed and well described and written in such a fashion that they are transparent and repeatable.

Weaknesses:

I only have one major issue, which is possibly a product of the structure requirements of the paper/journal. With the Results and Discussion, line 91 onwards. I understand the structure of the paper necessitates delving immediately into the results, but it is quite hard to follow due to lack of background information. In comparison to the Methods, which are incredibly detailed, the Results in the main section read quite superficial. They provide broad overviews of broad findings but I found it very hard to actually get a picture of the main results in its current form. For example, how the different species factor in, etc.

The authors have done a good job of responding to the reviewer's comments, and the paper is now much improved.

https://doi.org/10.7554/eLife.103971.2.sa2

Reviewer #2 (Public review):

I would like to thank the authors for the revision and the input they invested in this study.

With the revised text of the study, my earlier criticism holds, and your arguments about the counterfactual approach are irrelevant to that. The recent rise of the counterfactual approach might likely mirror the fact that there are too many scientists behind their computers, and few go into the field to collect in situ data. Studies like the one presented here are a good intellectual exercise but the real impact is questionable. All your main conclusions are inferred from published studies on 7! bird species. In addition, spatial sampling in those seven species was not ideal in relation to your target questions. Thus, no matter how fancy your findings look, the basic fact remains that your input data were for 7 bird species only! Your conclusion, „our study provides a novel understanding of how QTP shapes migration patterns of birds, " is simply overstretching.

The way you respond to my criticism on L 81-93 is something different than what you admit in the rebuttal letter. The text of the ms is silent about the drawbacks and instead highlights your perspective. I understand you; you are trying to sell the story in a nice wrapper. In the rebuttal you state: „we assume species' responses to environments are conservative and their evolution should not discount our findings." But I do not see that clearly stated in the main text.

In your rebuttal, you respond to my criticism of "No matter how good the data eBird provides is, you do not know population-specific connections between wintering and breeding sites" when you responded: ... "we can track the movement of species every week, and capture the breeding and wintering areas for specific populations" I am having a feeling that you either play with words with me or do not understand that from eBird data nobody will be ever able to estimate population-specific teleconnections between breeding and wintering areas. It is simply impossible as you do not track individuals. eBird gives you a global picture per species but not for particular populations. You cannot resolve this critical drawback of your study. I am sorry that you invested so much energy into this study, but I see it as a very limited contribution to understanding the role of a major barrier in shaping migration.

My modest suggestion for you is: go into the field. Ideally use bird radars along the plateau to document whether the birds shift the directions when facing the barrier.

https://doi.org/10.7554/eLife.103971.2.sa1

Author response:

The following is the authors' response to the previous reviews

> ***eLife Assessment***
>
> *This study addresses a novel and interesting question about how the rise of the Qinghai-Tibet Plateau influenced patterns of bird migration, employing a multi-faceted approach that combines species distribution data with environmental modeling. The findings are*

> *valuable for understanding avian migration within a subfield, but the strength of evidence is incomplete due to critical methodological assumptions about historical species-environment correlations, limited tracking data, and insufficient clarity in species selection criteria. Addressing these weaknesses would significantly enhance the reliability and interpretability of the results.*

We would like to thank you and two anonymous reviewers for your careful, thoughtful, and constructive feedback on our manuscript. These reviews made us revisit a lot of our assumptions and we believe the paper is much improved as a result. In addition to minor points, we have made three main changes to our manuscript in response to the reviews. First, we addressed the concerns on the assumptions of historical species-environment correlations from perspectives of both theoretical and empirical evidence. Second, we discussed the benefits and limitations of using tracking data in our study and demonstrate how the findings of our study are consolidated with results of previous studies. Third, we clarified our criteria for selecting species in terms of both eBird and tracking data.

Below, we respond to each comment in turn. Once again, we thank you all for your feedback.

> ***Public Reviews:***
>
> ***Reviewer #1 (Public review):***
>
> *Strengths:*
>
> *This is an interesting topic and a novel theme. The visualisations and presentation are to a very high standard. The Introduction is very well-written and introduces the main concepts well, with a clear logical structure and good use of the literature. The methods are detailed and well described and written in such a fashion that they are transparent and repeatable.*

We are appreciative of the reviewer’s careful reading of our manuscript, encouraging comments and constructive suggestions.

> *Weaknesses:*
>
> *I only have one major issue, which is possibly a product of the structure requirements of the paper/journal. This relates to the Results and Discussion, line 91 onwards. I understand the structure of the paper necessitates delving immediately into the results, but it is quite hard to follow due to a lack of background information. In comparison to the Methods, which are incredibly detailed, the Results in the main section reads as quite superficial. They provide broad overviews of broad findings but I found it very hard to actually get a picture of the main results in its current form. For example, how the different species factor in, etc.*

Yes, it is the journal request to format in this way (Methods follows the Results and Discussion) for the article type of short reports. As suggested, in the revision we have elaborated on details of our findings, in terms of (i) shifts of distribution of avian breeding and wintering areas under the influence of the uplift of the Qinghai-Tibet Plateau (Lines 102-116), and (ii) major factors that shape current migration patterns of birds in the plateau (Lines 118-138). We have also better referenced the approaches we used in the study.

> ***Reviewer #2 (Public review):***
>
> *Summary:*

> *The study tries to assess how the rise of the Qinghai-Tibet Plateau affected patterns of bird migration between their breeding and wintering sites. They do so by correlating the present distribution of the species with a set of environmental variables. The data on species distributions come from eBird. The main issue lies in the problematic assumption that species correlations between their current distribution and environment were about the same before the rise of the Plateau. There is no ground truthing and the study relies on Movebank data of only 7 species which are not even listed in the study. Similarly, the study does not outline the boundaries of breeding sites NE of the Plateau. Thus it is absolutely unclear potentially which breeding populations it covers.*

We are very grateful for the careful review and helpful suggestions. We have revised the manuscript carefully in response to the reviewer's comments and believe that it is much improved as a result. Below are our point-by-point replies to the comments.

> *Strengths:*
>
> *I like the approach for how you combined various environmental datasets for the modelling part.*

We appreciate the reviewer's encouragement.

> *Weaknesses:*
>
> *The major weakness of the study lies in the assumption that species correlations between their current distribution and environments found today are back-projected to the far past before the rise of the Q-T Plateau. This would mean that species responses to the environmental cues do not evolve which is clearly not true. Thus, your study is a very nice intellectual exercise of too many ifs.*

This is a valid concern. We have addressed this from both the perspectives of the theoretical design of our study and empirical evidence.

First, we agree with the reviewer that species responses to environmental cues might vary over time. Nonetheless, the simulated environments before the uplift of the plateau serve as a counterfactual state in our study. Counterfactual is an important concept to support causation claims by comparing what happened to what would have happened in a hypothetical situation: "If event X had not occurred, event Y would not have occurred" (Lewis 1973). Recent years have seen an increasing application of the counterfactual approach to detect biodiversity change, i.e., comparing diversity between the counterfactual state and real estimates to attribute the factors causing such changes (e.g., Gonzalez et al. 2023). Whilst we do not aim to provide causal inferences for avian distributional change, using the counterfactual approach, we are able to estimate the influence of the plateau uplift by detecting the changes of avian distributions, i.e., by comparing where the birds would have distributed without the plateau to where they currently distributed. We regard the counterfactual environments as a powerful tool for eliminating, to the extent possible, vagueness, as opposed to simply description of current distributions of birds. Therefore, we assume species' responses to environments are conservative and their evolution should not discount our findings. We have clarified this in the Introduction (Lines 81-93).

Second, we used species distribution modelling to contrast the distributions of birds before and after the uplift of the plateau under the assumption that species tend to keep their ancestral ecological traits over time (i.e., niche conservatism). This indicates a high probability for species to distribute in similar environments wherever suitable. Particularly, considering bird distributions are more likely to be influenced by food resources and vegetation distributions (Qu et al. 2010, Li et al. 2021, Martins et al. 2024), and the available food and vegetation before the uplift can provide suitable habitats for birds (Jia et al. 2020), we believe the findings can provide valuable insights into the influence of the plateau rise on avian migratory patterns. Having said that, we acknowledge other factors, e.g., carbon dioxide concentrations (Zhang et al. 2022), can influence the simulations of environments and our prediction of avian distribution. We have clarified the assumptions and evidence we have for the modelling in Methods (Lines 362-370).

> *The second major drawback lies in the way you estimate the migratory routes of particular birds. No matter how good the data eBird provides is, you do not know population-specific connections between wintering and breeding sites. Some might overwinter in India, some populations in Africa and you will never know the teleconnections between breeding and wintering sites of particular species. The few available tracking studies (seven!) are too coarse and with limited aspects of migratory connectivity to give answer on the target questions of your study.*

We agree with the reviewer that establishing interconnections for birds is important for estimating the migration patterns of birds. We employed a dynamic model to assess their weekly distributions. Thus, we can track the movement of species every week, and capture the breeding and wintering areas for specific populations. That being said, we acknowledge that our approach can be subjected to the patchy sampling of eBird data. In contrast, tracking data can provide detailed information of the movement patterns of species but are limited to small numbers of species due to the considerable costs and time needed. We aimed to adopt the tracking data to examine the influence of focal factors on avian migration patterns, but only seven species, to the best of our ability, were acquired. Moreover, similar results were found in studies that used tracking data to estimate the distribution of breeding and wintering areas of birds in the plateau (e.g., Prosser et al. 2011, Zhang et al. 2011, Zhang et al. 2014, Liu et al. 2018, Kumar et al. 2020, Wang et al. 2020, Pu and Guo 2023, Yu et al. 2024, Zhao et al. 2024). We believe the conclusions based on seven species are rigour, but their implications could be restricted by the number of tracking species we obtained. We have better demonstrated how our findings on breeding and wintering areas of birds are reinforced by other studies reporting the locations of those areas. We have also added a separate caveat section to discuss the limitations stated above (Lines 202-215).

> *Your set of species is unclear, selection criteria for the 50 species are unknown and variability in their migratory strategies is likely to affect the direction of the effects.*

In this revision, we have clarified the selection criteria for the 50 species and outlined the boundaries of the breeding areas of all birds (Lines 243-249). Briefly, we first obtained a full list of birds in the plateau from Prins and Namgail (2017). We then extracted species identified as full migrants in Birdlife International (https://datazone.birdlife.org/species/spcdistPOS) from the full list. Migratory birds may follow a capital or income migratory strategy depending on how much birds ingest endogenous reserved energy gained prior to reproduction. We have added discussions on how these migratory strategies might influence the effects of environment on migratory direction (Lines 183-200).

> *In addition, the position of the breeding sites relative to the Q-T plate will affect the azimuths and resulting migratory flyways. So in fact, we have no idea what your estimates mean in Figure 2.*

We calculated the azimuths not only by the angles between breeding sites and wintering sites but also based on the angles between the stopovers of birds. Therefore, the azimuths are influenced by the relative positions of breeding, wintering and stopover sites. This would minimize the possible errors by just using breeding areas such as the biases caused by relative locations of breeding areas to the QTP as the reviewer pointed. We have better explained this both in the Introduction, Methods and legend of Figure 2.

> *There is no way one can assess the performance of your statistical exercises, e.g. performances of the models.*

As suggested, we have reported Area Under the Curve (AUC) of the Receiver Operator Characteristic (ROC)assess the performances of the models (Table S1). AUC is a threshold-independent measurement for discrimination ability between presence and random points (Phillips et al. 2006). When the AUC value is higher than 0.75, the model was considered to be good (Elith et al. 2006). (Lines 379-383).

> ***Recommendations for the authors:***
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> ***Reviewer #1 (Recommendations for the authors):***
>
> *This is an interesting topic and a novel theme. The visualisations and presentation are to a very high standard. The Introduction is very well-written and introduces the main concepts well, with a clear logical structure and good use of the literature. The Methods are detailed and well described and written in such a fashion that they are transparent and repeatable.*
>
> *I only have one major issue, which is possibly a product of the structure requirements of the paper/journal. With the Results and Discussion, line 91 onwards. I understand the structure of the paper necessitates delving immediately into the results, but it is quite hard to follow due to a lack of background information. In comparison to the Methods, which are incredibly detailed, the Results in the main section read quite superficial. They provide broad overviews of broad findings but I found it very hard to actually get a picture of the main results in its current form. For example, how the different species factor in, etc.*

Please see our responses above.

> ***Reviewer #2 (Recommendations for the authors):***
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> *Methodological issues:*
>
> *Line 219 Why have you selected only 64 species and what were the selection criteria?*

We have clarified the selection criteria (Lines 243-248). Briefly, we first obtained a full list of birds in the plateau from Prins and Namgail (2017). We then extracted species identified as full migrants in Birdlife International (https://datazone.birdlife.org/species/spcdistPOS) from the full list.

> *Minor:*
>
> *Line 219 eBird has very uneven distribution, especially in vast areas of Russia. How can your exercise on Lines 232-238 overcome this issue?*

Yes, eBird data can be biased due to patchy sampling and variation of observers’ skills in identifying species. To address this issue, we have developed an adaptive spatial-temporal modelling (stemflow; Chen et al. 2024) to correct the imbalance distribution of data and modelled the observer experience to address the bias in recognising species. The stemflow was developed based on a machine learning modelling framework (AdaSTEM) which leverages the spatio-temporal adjacency information of sample points to model occurrence or abundance of species at different scales. It has been frequently used in modelling eBird data

(Fink et al. 2013, Johnston et al. 2015, Fink et al. 2020) and has been proven to be efficient and advanced in multi-scale spatiotemporal data modelling. We have better explained this (Lines 251-270; Lines 307-321).

> *Line 54 This sentence sounds very empty and in fact does not tell us much.*

We have adjusted this sentenced to “Animal movement underpins species’ spatial distributions and ecosystem processes”.

> *Line 55 Again a sentence that implies a causality of the annual cycle to make the species migrate. It does not make sense.*

We have revised this sentence as “An important animal movement behaviour is migrating between breeding and wintering grounds”.

> *Line 58 How is our fascination with migratory journeys related to the present article? I think this line is empty.*

We have changed this sentence to “Those migratory journeys have intrigued a body of different approaches and indicators to describe and model migration, including migratory direction, speed, timing, distance, and staging periods”.

> *Figure 1 - ABC insets are OK, but a combination of lati- and longitudinal patterns is possible, e.g. in species with conservative strategies or for whatever other reason.*

Thank you for the suggestion. We kept the ABC insets rather than combining them together as we believe this can deliver a clear structure of influence of QTP uplift under different scenarios.

> *The legend to Figure 2 is not self-explanatory. Please make it clear what the response variable is and its units. The first line of the legend should read something like The influence of environmental factors on the direction of avian migration.*

Thank you. We have amended the legends of Figure 2 as suggested:

“Figure 2. The influence of environmental factors on the direction of avian migration. Migratory directions are calculated based on the azimuths between each adjacent stopover, breeding and wintering areas for each species. We employ multivariate linear regression models under the Bayesian framework to measure the correlation between environmental factors and avian migratory directions. Wind represents the wind cost calculated by wind connectivity. Vegetation is measured by the proportion of average vegetation cover in each pixel (~1.9° in latitude by 2.5° in longitude). Temperature is the average annual temperature. Precipitation is the average yearly precipitation. All environmental layers are obtained using the Community Earth System Model. West QTP, central QTP, and East QTP denote areas in the areas west (longitude < 73°E), central (73°E ≤ longitude < 105°E), and east of (longitude ≥ 105°E) the Qinghai-Tibet Plateau, respectively.”

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