RESEARCH ARTICLE

Global Change Biology **WILEY**

Spatially heterogeneous shifts in vegetation phenology induced by climate change threaten the integrity of the avian migration network

Jie Wei[1] | Fei Xu[2] | Ella F. Cole[3] | Ben C. Sheldon[3] | Willem F. de Boer[4] | Ben Wielstra[5,6] | Haohuan Fu[1] | Peng Gong[1,7] | Yali Si[1,8]

[1]Ministry of Education Ecological Field Station for East Asian Migratory Birds, Department of Earth System Science, Tsinghua University, Beijing, China

[2]Key Laboratory of the Three Gorges Reservoir Region's Eco-Environment, Ministry of Education, Chongqing University, Chongqing, China

[3]Edward Grey Institute, Department of Biology, University of Oxford, Oxford, UK

[4]Wildlife Ecology and Conservation Group, Wageningen University and Research, Wageningen, the Netherlands

[5]Institute of Biology Leiden, Leiden University, Leiden, the Netherlands

[6]Naturalis Biodiversity Center, Leiden, the Netherlands

[7]Department of Geography, Department of Earth Sciences, Institute for Climate and Carbon Neutrality, The University of Hong Kong, Hong Kong, China

[8]Institute of Environmental Sciences, Leiden University, Leiden, the Netherlands

Correspondence
Fei Xu, Key Laboratory of the Three Gorges Reservoir Region's Eco-Environment, Ministry of Education, Chongqing University, Chongqing, China.
Email: feixu@cqu.edu.cn

Peng Gong, Department of Geography, Department of Earth Sciences, Institute for Climate and Carbon Neutrality, The University of Hong Kong, Hong Kong, China.
Email: penggong@hku.hk

Yali Si, Institute of Environmental Sciences, Leiden University, Leiden, the Netherlands.
Email: y.si@cml.leidenuniv.nl

Funding information
China Scholarship Council, Grant/Award Number: 201906210103; National Natural Science Foundation of China, Grant/Award Number: 41471347 and 42301055

Abstract

Phenological responses to climate change frequently vary among trophic levels, which can result in increasing asynchrony between the peak energy requirements of consumers and the availability of resources. Migratory birds use multiple habitats with seasonal food resources along migration flyways. Spatially heterogeneous climate change could cause the phenology of food availability along the migration flyway to become desynchronized. Such heterogeneous shifts in food phenology could pose a challenge to migratory birds by reducing their opportunity for food availability along the migration path and consequently influencing their survival and reproduction. We develop a novel graph-based approach to quantify this problem and deploy it to evaluate the condition of the heterogeneous shifts in vegetation phenology for 16 migratory herbivorous waterfowl species in Asia. We show that climate change-induced heterogeneous shifts in vegetation phenology could cause a 12% loss of migration network integrity on average across all study species. Species that winter at relatively lower latitudes are subjected to a higher loss of integrity in their migration network. These findings highlight the susceptibility of migratory species to climate change. Our proposed methodological framework could be applied to migratory species in general to yield an accurate assessment of the exposure under climate change and help to identify actions for biodiversity conservation in the face of climate-related risks.

1 | INTRODUCTION

Phenology is the timing of life-history events, such as the germinating and flowering of plants, and the migrating and breeding of animals. Shifts in phenology in response to climate changes are readily observed and impact fitness by altering the abiotic and biotic conditions experienced by individuals (Cohen et al., 2018; Walther et al., 2002). Such shifts show considerable variation across regions, biomes, and trophic levels (Kharouba et al., 2018; Thackeray et al., 2016). Heterogeneous shifts in phenology could disrupt the match between the activity of consumers and the abundance period of their food. This phenomenon is known as phenological 'mismatch' or asynchrony (Johansson et al., 2015; Samplonius et al., 2021). Phenological asynchrony could negatively impact the demography of species and in turn the functioning of ecosystems (Miller-Rushing et al., 2010; Youngflesh et al., 2023).

Migratory birds travel between distinct wintering and breeding grounds and often make stopovers at multiple, geographically distant areas along their migration paths to replenish their reserves (Newton, 2008). Migrants replenish their energy reserves and arrive at their breeding ground in prime condition by tracking the peak in local food availability along their flyway (Drent et al., 2006). If a shift in phenology of food resources is consistent across space, birds might be able to accommodate this, for instance by simply changing the onset of migration accordingly (Figure 1). However, climate change is uneven in space and, as a consequence, phenological shifts of food resources might be spatially heterogeneous (Jeong et al., 2011; Mayor et al., 2017). Under heterogeneous shifts in food phenology, food availability along the migration routes might deteriorate (Figure 1). Birds tend to follow a risk-averse strategy and select areas with abundant food at the time of foraging (Anderson et al., 2012) and/or with a constant and predictable food supply over time (Bauer et al., 2008). Local food phenology is often used as a coarse indicator for food availability and a cue to calibrate migration timing towards the next area, among other cues including photoperiod and departure time from wintering area (Duriez et al., 2009; Newton, 2008). Therefore, heterogeneous shifts of food phenology in space result in a reduced predictability of the food supply. Hence, asynchrony between migration timing and local food availability among wintering, stopover and breeding areas is expected to negatively affect individual fitness (Knudsen et al., 2011).

Previous studies investigating the impact of shifts in food phenology on migratory birds mainly focused on the breeding area (Fang et al., 2021; Knudsen et al., 2011; Marra et al., 2015; Radchuk et al., 2019) and few have considered the entire migration route (Emmenegger et al., 2016; Kellermann & van Riper, 2015; Mayor et al., 2017; Youngflesh et al., 2021). For an accurate evaluation of the effect of climate change-induced heterogeneous shifts in food phenology, we argue that it is critical to take the shift in food phenology along the entire migration network (including wintering, stopover, and breeding areas) into account.

Spatially heterogeneous shifts in vegetation phenology can be quantified in several ways (Figure 1): (1) by the difference of long-term change trends in the vegetation phenology (advanced or delayed in the change direction and the magnitude of change) between areas (Emmenegger et al., 2016); (2) by the strength of correlations in the phenological shifts between areas (phenological correlation coefficient) (Tombre et al., 2008); (3) by the proportionality index, which estimates the slope of a standardized major axis regression between the annual anomaly of the onset of spring for the current and the previous area visited (with a higher value indicating that the condition of the current area is better predicted based on the condition of the previous area visited) (Kolzsch et al., 2015); and (4) by the interannual fluctuation of vegetation phenology at the destination area, which is the change in variance over time (i.e., the variability of deviation from the long-term mean) (Kolzsch et al., 2015). Climate change-induced heterogeneous shifts in food phenology would negatively affect the movement probability in the migration network, resulting in a decreased network integrity; potentially even its collapse (Figure 1). Therefore, we propose to quantify the effect of climate change-induced heterogeneous shifts in food phenology by the change of integrity of the migration network when taking the phenological shifts among habitat areas into account.

Here we select 16 migratory herbivorous waterfowl species based on their distribution ranges, migration and foraging attributes, and quantify heterogeneous shifts in vegetation phenology along their migration routes. We focus on the Asia-Pacific region, covering the Central Asian, East Asian-Australasian, and West Pacific flyways (Figure S1), and identify suitable wetland areas between wintering and breeding grounds based on species-specific habitat requirements using species distribution modelling. We then set the suitable wetland areas as the nodes in the migration network. Two geographical metrics i.e., between-node distance (BD) and between-node angle (BA), and four vegetation phenology metrics i.e., between-node change trend difference (BTD), between-node correlation strength (BCS), between-node proportionality index (BPI) of the onset of spring, and node-level interannual fluctuation (NIF) of the onset of spring are used to determine the integrity of the migration network in facilitating movement. Specifically, we quantify the change in the network integrity under two circumstances: when assuming no climate change over the period of 2000–2020 and when using observed heterogeneous shifts in vegetation phenology derived from satellite imagery for the same period (Figure S1). Our aim is to (1) develop a methodological framework to quantify the degree to which climate change-induced heterogeneous shifts in vegetation phenology threaten the integrity of migration networks, and (2) investigate the effect of spatial factors on the change of migration network integrity for different species.
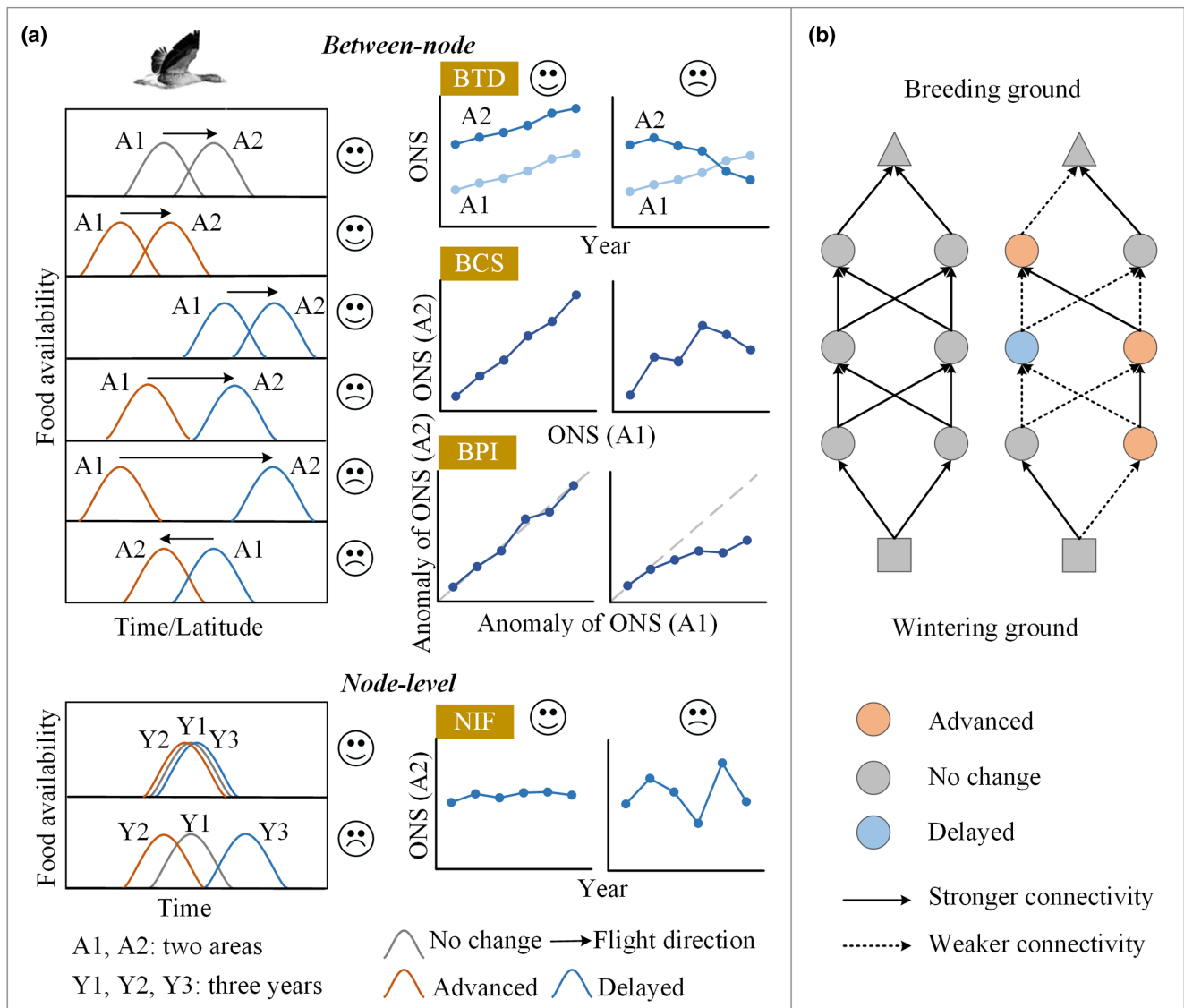
FIGURE 1 Schematic illustration showing how climate change-induced heterogeneous shifts in food phenology reduce migration network integrity. (a) Two areas (A1 and A2) consecutively visited during migration have consecutive food peaks. Heterogeneous shifts in food phenology between A1 and A2 (referring to the onset of spring in this study), reflected by the increased between-node change trend difference (BTD) and the decreased between-node correlation strength (BCS) and between-node proportionality index (BPI), may result in a potential asynchrony between bird migration timing and peak availability of food, leading to reduced or no suitable food at A2. Separately, at the node level, areas with dramatic change in food phenology among years (Y1, Y2, and Y3), reflected by the increased node-level interannual fluctuation (NIF), may result in a higher chance of phenological asynchrony, in comparison to areas with subtle changes among years. (b) The movement probability of a migrant is lower among areas with a different level of shift in food phenology, which threatens the integrity of the migration network.

2 | MATERIALS AND METHODS

2.1 | Study area and species

The Asia-Pacific region comprises three recognized migratory waterbird flyways, the Central Asian, East Asian-Australasian, and West Pacific Flyway (Figure S1). This region supports large number of waterbirds and the highest proportion of declining populations (Wetlands International, 2012). At least 243 migratory waterbird species are recorded in this region, including 49 threatened species (Mundkur, 2006).

Anatidae (geese, ducks, and swans; hereafter waterfowl) is the largest family of waterbirds. We used the species list of migratory waterfowl and bird species distribution maps from Birdlife International (BirdLife International and NatureServe, 2020) to select the species distributed in the Asia-Pacific region. Herbivorous species was defined by the species-level foraging attributes of the world's birds (Wilman et al., 2014), including the diet and foraging strata. A threshold of ≥50% diet of plant materials (e.g., grass, reeds, and moss, but excluding fruit, nectar and seed) was used to include species, and then we further selected species with percentage of

foraging on above ground vegetation (i.e., a foraging stratum of foraging on ground) larger than zero. A total of 16 species were included in this study (Table S3).

2.2 | Bird data

We obtained bird occurrence data for 16 study species within the study area from the eBird Basic Dataset (EBD, version released in February 2019, www.ebird.org/science/download-ebird-data-products; Sullivan et al., 2014). eBird is a semi-structural citizen science project, which allows non-detections to be reported (La Sorte et al., 2018). We used complete checklists and only included those with less than 6 h of observation duration and 10 km travel distance, and with 10 or fewer observers (Johnston et al., 2021). Scientific name, longitude, latitude, and observation date from the checklists were extracted to predict suitable area for each study species. We used bird occurrence from 2000 to 2018 to increase the sample size (Table S6).

2.3 | Environmental data

We obtained datasets on wetland, land cover and elevation to estimate the suitable habitat for the selected species. The Global Lakes and Wetlands Database (GLWD-1 and GLWD-2) was used to delineate the boundary of wetlands, which comprises polygons of lakes, reservoirs and smaller water bodies with a surface area no smaller than 0.1km^2 (Lehner & Doll, 2004). The 300-m annual global land cover datasets are from European Space Agency (ESA) Climate Change Initiative (CCI) product for 2000–2015 (European Space Agency, 2017), and European Centre (EC) Copernicus Climate Change Service (CS3) product for 2016–2020 (European Centre, 2020). These two products use a consistent processing method and describe the land surface in 22 classes under the United Nations Food and Agriculture Organization's (UN FAO) Land Cover Classification System (LCCS). The Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010) with a 7.5-arc-second spatial resolution was used, which incorporates the best available global elevation data (Danielson & Gesch, 2011). To quantify the vegetation phenology change, we derived the Enhanced Vegetation Index (EVI) from the 8-day 250-metre Moderate Resolution Imaging Spectroradiometer (MODIS) Terra surface reflectance product (MOD09Q1; v6.0) (Vermote et al., 2015), and further calculated the onset of spring from 2000 to 2020.

2.4 | Constructing the wetland-based migration network

A bird migration network is composed of a set of areas with suitable habitats (i.e., nodes) and the connection between paired nodes (i.e., the edge) representing the probability of movement between each pair of nodes (i.e., the weight of edges). We firstly defined the study area of each species as the minimum convex polygon (MCP) around the species distribution maps from BirdLife International. The species distribution maps from BirdLife International delineate the wintering and breeding ranges, and for some species also the passage ranges (i.e., areas where a species likely occurs regularly on migration for a relatively short period). However, these are rough ranges and also include unsuitable areas for the study species. We therefore modelled suitable area for each species using species distribution modelling, to be used as nodes in the migration network.

We constructed generalized additive models (GAMs) to capture the nonlinear responses of bird occurrence at the different areas using eight relevant environmental factors. We extracted six land cover variables for each bird record from the land cover map of the same year, including the size of croplands [representing alterative habitat areas as birds use farmland in the core stopover areas (Si et al., 2018; Si et al., 2020)], the size of waterbodies, the sum of the grasslands and flooded vegetation (representing potential foraging areas), the sum of grasslands, flooded vegetation, and water bodies (representing potential foraging and roosting areas), and the sum of grasslands, flooded vegetation, shrublands, and sparse vegetation (representing herbaceous areas), and the sum of grasslands, flooded vegetation, shrublands, sparse vegetation, and water bodies (representing the total habitat). We also included two geographical variables covering elevation and longitude (to control for differences in the width of the migration corridor). We then built separate GAMs for each species in each region, that is, breeding, stopover, wintering regions and subregions when the range of latitude exceed 30 degrees. Further details on bird data processing, species distribution modelling, and predicting the suitable wetland areas are provided in the Supplementary Methods in Data S1.

2.5 | Calculating the vegetation phenology over time

To quantify the vegetation development stages, we only used the herbaceous areas (including grassland, shrubland, flooded vegetation, and sparse vegetation) to represent the phenology of the potential foraging land in the wetland areas (nodes). The two-band EVI was calculated according to Equation (1):

$$EVI = 2.5 \frac{N - R}{N + 2.4R + 1}, \qquad (1)$$

where N and R are the surface reflectance in near-infrared and red bands, respectively (Jiang et al., 2008). Cloud-contaminated observations were removed based on the quality control layer. We used the Savitzky–Golay fitting method with a window size of eight to smooth the EVI time series in TIMESAT software to reduce noise (Eklundh & Jönsson, 2015; Jönsson & Eklundh, 2002, 2004). For each eight-day period, we then calculated the change rate using the smoothed annual EVI time series. The date (in Julian days) with the largest change rate was regarded as the onset of spring (Reed & Ohlen, 1994). Pixels with

the largest value of the yearly smoothed EVI time series of less than 0.2, were regarded as non-vegetated areas (Wei et al., 2019), and removed from the calculation.

2.6 | Defining the movement probability between nodes

Traditionally, the movement probability, that is, weight of the edge, is defined by geographic features of the migration network, commonly used the between-node Euclidean distance (BD). Because northward spring migration of the study species, we also took into account the between-node angle (BA) to give a higher movement probability on the northward movement. We also constructed four vegetation phenology metrics to further quantify the effect of heterogeneous shifts in vegetation phenology on the movement probability in the migration network: between-node change trend difference (BTD), between-node correlation strength (BCS), between-node proportionality index (BPI) of the onset of spring, and node-level interannual fluctuation (NIF) of the onset of spring. Because all study species adopt a mixed capital-income breeding strategy, which means they rely on food in both stopover and breeding areas to accumulate the energy required for breeding, we assume these metrics have an equally multiplicative effect on each species.

The weight of edges for the migration network is then calculated by Equation (2):

$$W_{ij} = BD_{ij} \times BA_{ij} \times \left(1 - BTD_{ij}\right) \times BCS_{ij} \times \left(1 - BPI_{ij}\right) \times \left(1 - NIF_{ij}\right), \quad (2)$$

where W_{ij} is the weight of the edge between nodes i and j with a movement direction from node i to j. BD_{ij}, and BA_{ij} (geographic metrics) are the movement probability from i to j, quantified by between-node Euclidean distance and between-node angle, respectively. Vegetation phenology metrics BTD_{ij}, BCS_{ij}, and BPI_{ij} are movement probability from node i to j quantified by the difference in phenology change among two nodes, whereas NIF_{ij} is quantified by the interannual fluctuation of phenology at node j.

BD was quantified by a decreasing exponential function (Urban & Keitt, 2001), indicating an increasing distance is related to a lower movement probability. BA was determined by the between-node angle where the highest movement probability is assigned to the northward movement and the lowest to the southward movement. For each node, the regression slope was defined as the change trend of the onset of spring for 2000–2020. BTD was the absolute value of the change trend difference between two nodes and was negatively associated with the movement probability. BCS was the Pearson correlation coefficient of the onset of spring over the 21 years between two nodes. The proportionality index is the slope of a standardized major axis regression between annual anomalies of the onset of spring for the current and previously visited area (Kolzsch et al., 2015). BPI was defined as the absolute value of the difference between proportionality index and value one, with a smaller value leading to a higher movement probability. NIF was defined as the interquartile range of the yearly onset of spring over the 21 years

at the destination node. Detailed information for the calculation of the geographic and vegetation phenology metrics are shown in the Supplementary Methods in Data S1.

2.7 | Movement probability under different levels of vegetation phenology shift

Two types of movement probability under different levels of vegetation phenology shifts were calculated. W0 was calculated assuming no climate change in the study period (only with the base level of annual fluctuation). Under this condition, the vegetation phenology metrics BTD_0 and BPI_0 approach zero (normalized to 0.05), and BCS_0 approaches one (normalized to 0.95). To calculate the base level of annual fluctuation, we first fitted a linear regression to the yearly onset of spring for 2000–2020 at each node, and then used the interquartile range of the residuals (rescaled to range between 0.05 and 0.95) to represent NIF_0. W1 was calculated using the observed heterogeneous shifts of vegetation phenology in the study period. BD, BA, BTD_1, BCS_1, BPI_1, and NIF_1 were rescaled to range between 0.05 and 0.95 to avoid the edge weight becoming zero when multiplying these metrics, and facilitate comparisons among species. The multicollinearity of all metrics was checked by calculating the Pearson correlation coefficient between each two metrics.

2.8 | Calculating the change of network integrity

We measured the functional connectivity (Saura et al., 2011) of the migration network with a graph-based habitat availability metric of Equivalent Connected Area (ECA). ECA is defined as the size of a single habitat node, which could provide the same level of connectivity as the actual network in the landscape (Equation (3)). A greater ECA indicates higher functional connectivity, thereby higher integrity of the migration network.

$$ECA = \sqrt{\sum_{i=1}^{n} \sum_{j=1}^{n} a_i a_j p_{ij}^*}, \quad (3)$$

where n is the total number of nodes in the migration network, and a is the size of the corresponding habitat node in square kilometres (referring to the averaged size of the suitable wetland area over the 21-year period). A path is a set of nodes as they bridge between nodes i and j, where each node can only be visited once. p_{ij} is the weight of the edge between nodes i and j, representing the probability of direct movement (i.e., without using any stepping stones) between two nodes. p_{ij}^* is the movement probability of the best path between nodes i and j, which has the maximum weight product of all edges than any other possible paths. When nodes i and j are close enough for direct movement, $p_{ij}^* = p_{ij}$. When they are distant and only connected by passing through one or more intermediate nodes, $p_{ij}^* > p_{ij}$.

Because the constructed bird migration networks were directional (the connection probability from node i to j was different

from that from node j to i), we used directed networks (Saura & Torné, 2009) to calculate the ECA. The change of ECA after considering the observed heterogeneous shifts in vegetation phenology in defining movement probability was calculated for each species:

$$\text{Change ratio}(\%) = \frac{\text{ECA}_{W1} - \text{ECA}_{W0}}{\text{ECA}_{W0}} \times 100, \quad (4)$$

where ECA_{W0} is the functional connectivity calculated by assuming no climate change and ECA_{W1} is the connectivity using observed heterogeneous shifts in vegetation phenology.

To investigate the contribution of each vegetation phenology metric in the change of the migration network integrity, the integrity change was also calculated by using each single vegetation phenology metric, respectively. For example, when evaluating the contribution of BTD, the weight of the edge between two nodes were quantified by two geographical metrics BD, BA and the specific phenology metric BTD. We used boxplots including non-outlier data range, median, and 25% and 75% lower and upper quartiles to show their difference.

2.9 | Analyzing the effect of spatial factors on migration network integrity change

To account for phylogenetic relatedness among species, we used a phylogenetic linear regression to test the effect of eight spatial variables on the variation of the mean network integrity change among species, covering migration distance, wintering and breeding latitudes, size of wintering and breeding ranges, migratory dispersion, number of habitat nodes, and migration corridor width. The migration distance (km) was the Euclidean distance between the centroids of the wintering and breeding ranges under the Asia North Equidistant Conic projection. Wintering and breeding latitudes were the latitudes of the centroids of the wintering and breeding ranges. The size of wintering and breeding ranges (km^2) were the total area of the wintering and breeding ranges using the Cylindrical Equal Area projection. The migratory dispersion was calculated as the difference between log-transformed wintering range size and breeding range size divided by log-transformed breeding range size, representing that the wintering range was relatively larger or smaller than the breeding range (Gilroy et al., 2016). The migration corridor width was measured as the total wetland areas (sum of the total habitat in each suitable wetland area), divided by the migration distance.

To reduce the multicollinearity, we only kept factors with a Variance Inflation Factor (VIF) smaller than 10; migration distance, wintering latitudes, size of breeding ranges, migratory dispersion, and migration corridor width were kept to fit the model (Figure S18). To account for phylogenetic relatedness among species, we used the Hackett backbone phylogenetic tree (Jetz et al., 2012). The change in network connectivity was modelled as a function of spatial variables by a phylogenetic linear model with stepwise selection. The amount of phylogenetic dependence among species was controlled by simultaneously computing a measure of phylogenetic signal in the

residuals of the models using Pagel's λ (Pagel, 1999). The best model was selected as the model with the smallest Akaike information criterion (AIC). The response curve of factors with a significant effect on the change of connectivity ($p < .05$) was predicted using the best model by changing the factor of interest while setting other factors constant at their median values.

The calculation of the vegetation phenology was performed in MATLAB R2020a (The MathWorks Inc., 2022). Mapping the suitable areas, defining the movement probability, calculating the effect of heterogeneous shifts in vegetation phenology on the network connectivity, and analyzing effects of spatial factors on the integrity change were performed in R 4.1.0 (R Core Team, 2021). The methodological framework for the whole analysis is shown in Figure S2.

3 | RESULTS

3.1 | Heterogeneous shifts of vegetation phenology across space

A wetland-based migration network was constructed based on suitable areas predicted by species distribution modelling (Supplementary Methods in Data S1) for each study species. The change of the onset of spring, in terms of both change trend (Figure 2; Figures S5–S13) and interannual fluctuation (Figure 3; Figures S14–S17) showed clear spatial heterogeneity. For areas with a significant change trend in the onset of spring over the study period (Figures S9–S12), most were advanced by less than a day per year (median: −0.77; interquartile range: −1.24 to 0.61). The interannual fluctuation of the onset of spring was lower in high latitudes, and most areas have a fluctuation of less than 20 days over the study period (median: 15; interquartile range: 12–23).

3.2 | Climate change-induced migration network integrity change

No severe multicollinearity was observed among these two geographic and four vegetation phenology metrics that weighted the movement probability (Table S1). Across all species, the level of migration network integrity decreased on average 11.94% (±4.11%; standard deviation) due to heterogeneous shifts in vegetation phenology (Figure 4a). All species were affected by heterogeneous shifts in vegetation phenology but the effect varied among species (Figure 4b). In general, tundra swan (*Cygnus columbianus*) had the most well-integrated migration network and Baikal teal (*Sibirionetta formosa*), the least. The effect on the change of integrity was highest for Chinese spot-billed duck (*Anas zonorhyncha*) and Baikal teal, particularly given that their migration networks were already poorly integrated. Some species, such as swan goose (*Anser cygnoides*) and cackling goose (*Branta hutchinsii*), were under a comparatively low influence but were still affected by the heterogenous shifts in vegetation phenology because of their originally poorly integrated
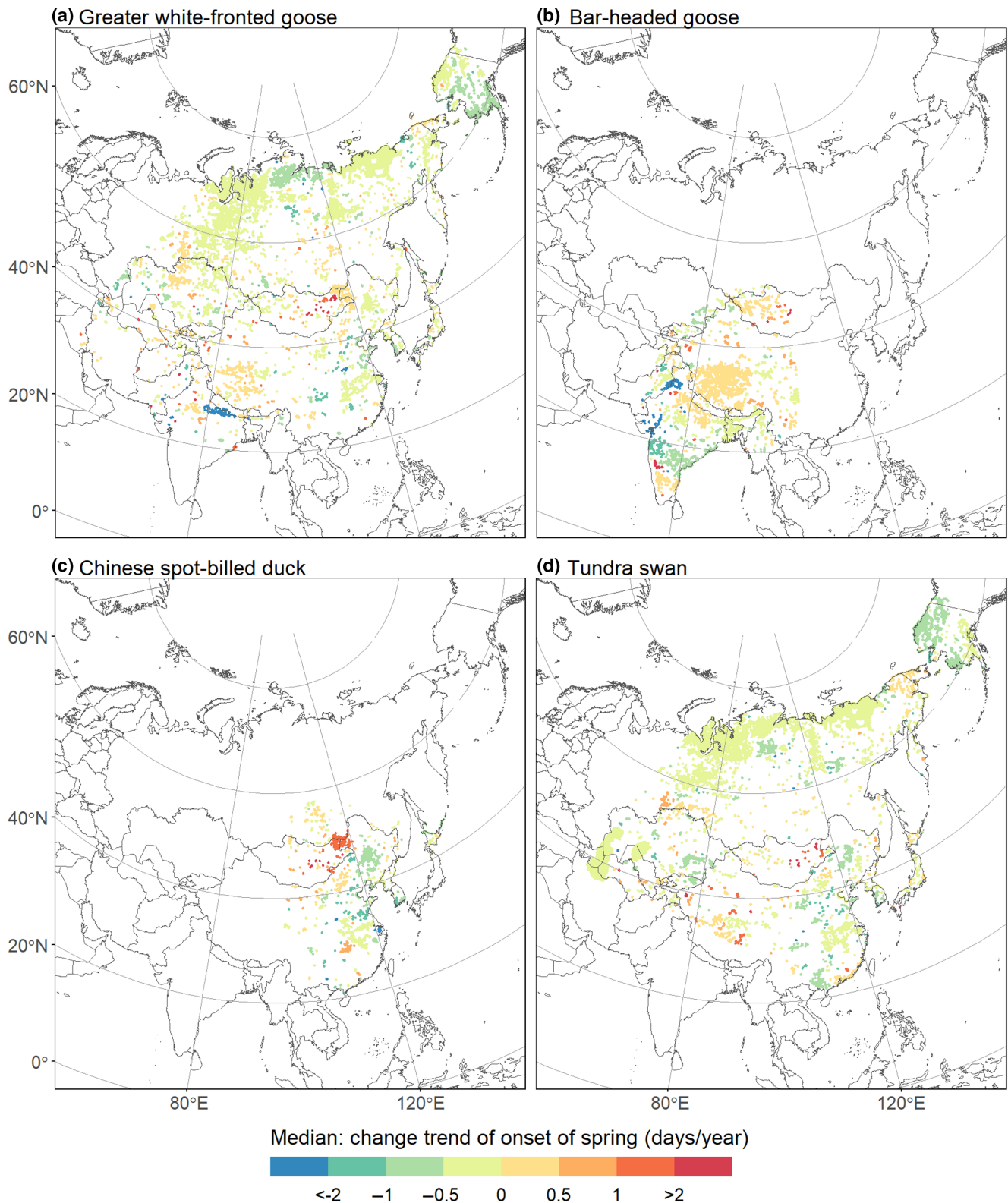
FIGURE 2 Change in the onset of spring from 2000 to 2020 across the bird migration network for four examples species. (a) Greater white-fronted goose (*Anser albifrons*), (b) bar-headed goose (*Anser indicus*), (c) Chinese spot-billed duck (*Anas zonorhyncha*), (d) Tundra swan (*Cygnus columbianus*). Conditions for all 16 Asian herbivorous waterfowl species (including median and the upper and lower quartiles) are shown in Figures S5–S8. Changes were defined as the rate of annual changes of the onset of spring over 21 years. A negative or positive value indicates an advanced or delayed onset of spring, irrespective of the level of significance. The value of each node is the median of the 99 permutations (99 random draws between the interquartile range of the onset of spring of herbaceous land within a node for each year results in 99 change trends for each node). Map lines delineate study areas and do not necessarily depict accepted national boundaries.
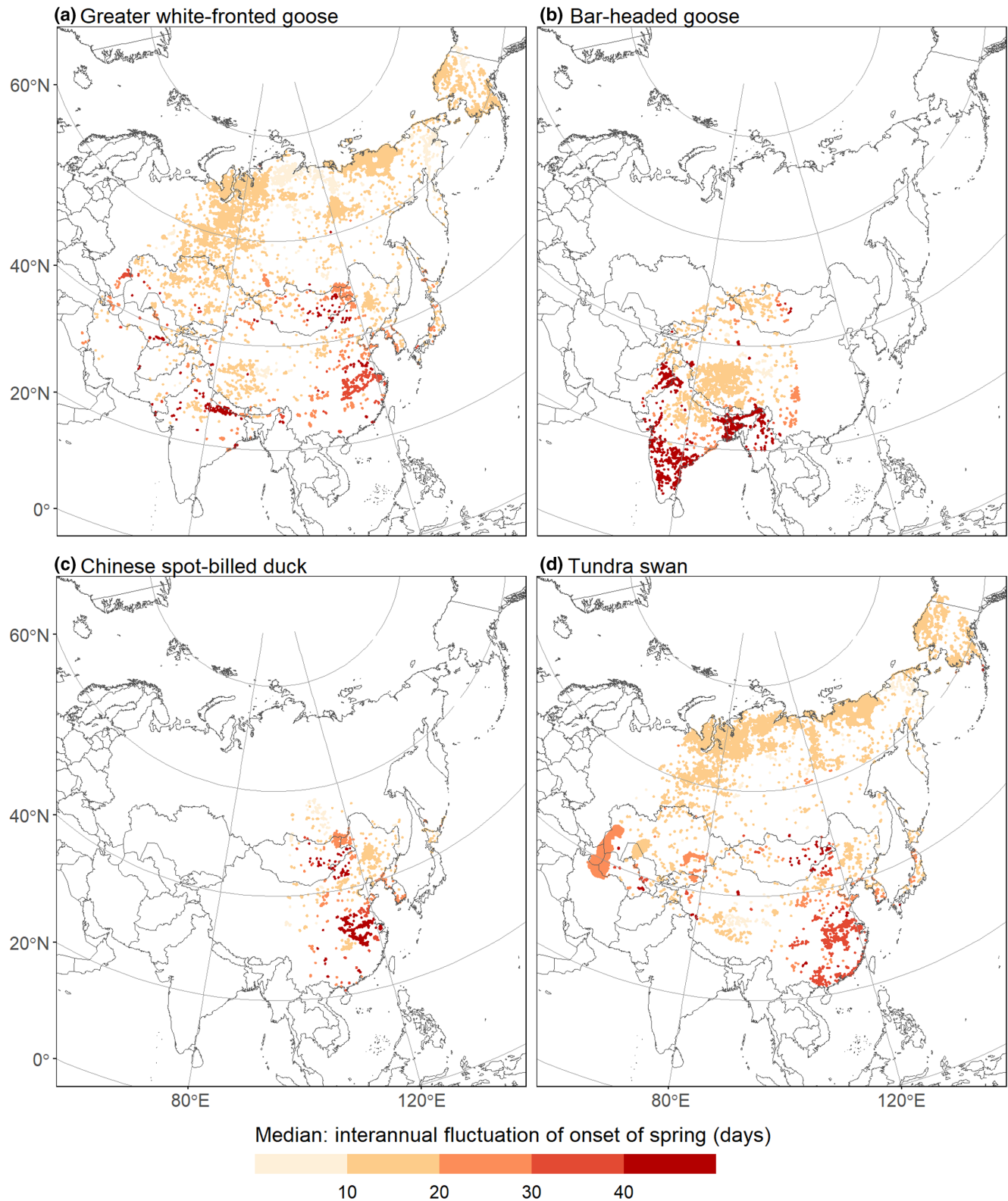
FIGURE 3 Interannual fluctuation in the onset of spring from 2000 to 2020 across the bird migration network for four example species. (a) Greater white-fronted goose (*Anser albifrons*), (b) bar-headed goose (*Anser indicus*), (c) Chinese spot-billed duck (*Anas zonorhyncha*), (d) Tundra swan (*Cygnus columbianus*). Conditions for all 16 Asian herbivorous waterfowl species (including median and the upper and lower quartiles) are shown in Figures S4–S7. Fluctuation is quantified by the interquartile range of the onset of spring over 21 years. Darker red indicates a higher fluctuation. The value of each node is the median of the 99 permutations (99 random draws between the interquartile range of the onset of spring of herbaceous land within a node for each year results in 99 fluctuation values for each node). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

migration networks. Among the four vegetation phenology metrics, a decrease in between-node correlation strength of the onset of spring led to the greatest connectivity loss of the migration network (Figure 5).

3.3 | Spatial factors related to the network integrity change

A relatively weak phylogenetic signal was detected in affecting the species-dependent integrity change, and wintering latitude showed a significant negative effect (Table S2). The effect of heterogeneous shifts in vegetation phenology on the change of

integrity was higher for species wintering at relatively lower latitudes (Figure 6).

4 | DISCUSSION

We propose a general methodological framework to quantify the exposure of migratory birds to climate change using a network-based approach. We find that all 16 Asian migratory herbivorous waterfowl species studied are affected by these heterogeneous shifts in vegetation phenology induced by climate change, with some being particularly threatened, reflected by the pronounced decrease of their migration network integrity. Species that winter
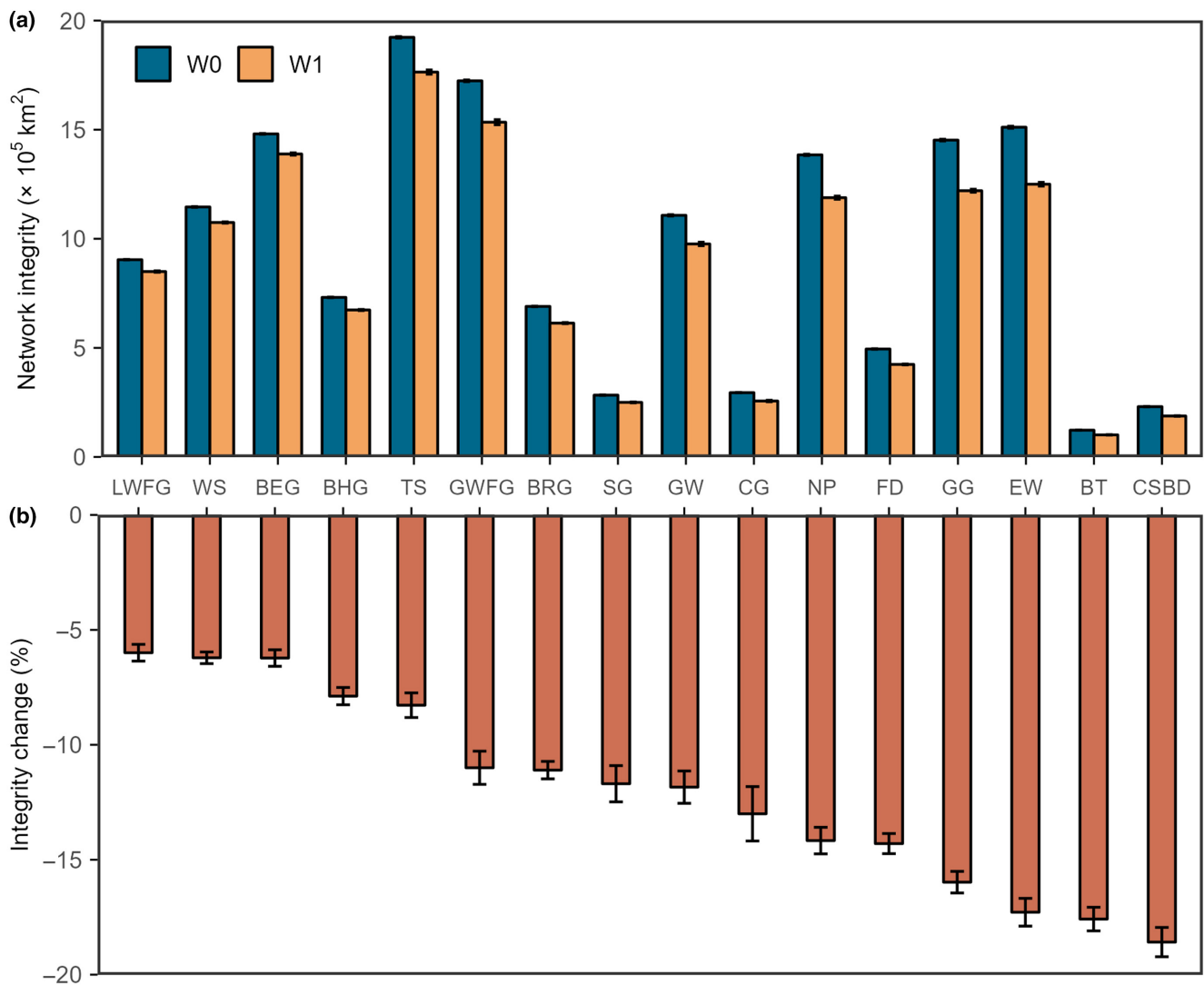

FIGURE 4 The integrity change of the migration network for 16 Asian herbivorous waterfowl species caused by climate change-induced heterogeneous shifts in vegetation phenology. (a) Integrity of the migration networks with the movement probability weighted by assuming no climate change in the study period (W0) and by using observed heterogeneous shifts in vegetation phenology (W1). (b) The species-specific percentage of network integrity change between W0 and W1. Error bar: the mean and standard deviation of the connectivity change (99 permutations accounting for the accumulating uncertainties from each step of analyses) for each study species. BEG, bean goose; BHG, bar-headed goose; BRG, brent goose; BT, Baikal teal; CG, cackling goose; CSBD, Chinese spot-billed duck; EW, Eurasian wigeon; FD, falcated duck; GG, greylag goose; GW, gadwall; GWFG, greater white-fronted goose; LWFG, lesser white-fronted goose; NP, northern pintail; SG, swan goose; TS, tundra swan; WS, whooper swan. The scientific names of the species are in Table S3.
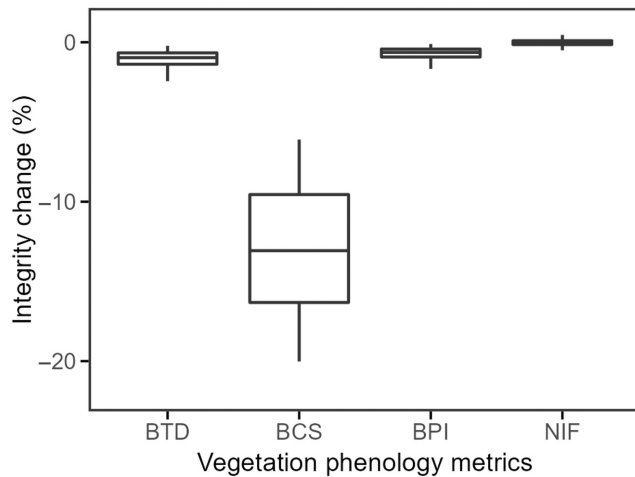
FIGURE 5 Contribution of individual vegetation phenology metric on the integrity change of the migration network for 16 Asian migratory herbivorous waterfowl species. The non-outlier data range, the median, and the 25% and 75% lower and upper quartiles are shown in boxplots. BCS: between-node correlation strength of the onset of spring; BPI: between-node proportionality index of the onset of spring; BTD: between-node change trend difference of the onset of spring; NIF: node-level interannual fluctuation of onset of spring.
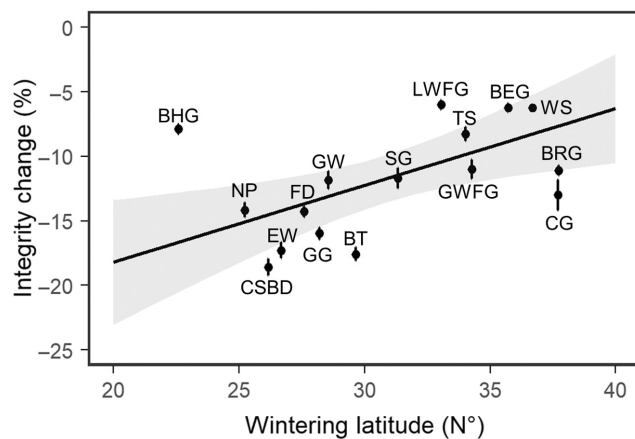

FIGURE 6 Effect of wintering latitude on the change of migration network integrity for 16 Asian herbivorous waterfowl species. Species wintering at relatively lower latitude are associated with a larger decrease in integrity. Gray areas show 95% confidence intervals of the predicted level of change by the best-fitting phylogenetic linear model. Error bar: the mean and standard deviation of the integrity change (99 permutations accounting for accumulating uncertainties from the previous steps of analyses). BEG, bean goose; BHG, bar-headed goose; BRG, brent goose; BT, Baikal teal; CG, cackling goose; CSBD, Chinese spot-billed duck; EW, Eurasian wigeon; FD, falcated duck; GG, greylag goose; GW, gadwall; GWFG, greater white-fronted goose; LWFG, lesser white-fronted goose; NP, northern pintail; SG, swan goose; TS, tundra swan; WS, whooper swan. The scientific names of the species are in Table S3.

at relatively lower latitude experience a larger network integrity loss. Our findings underline the risk that migratory species encounter due to spatially heterogeneous climate change and offer critical

information in protecting this unique group of species under climate change.

Climate change-induced heterogeneous shifts in vegetation phenology are observed along the migration routes of all study species. In accordance with the general trend of global warming (Piao et al., 2019), majority nodes in the migration networks show an advanced trend in the onset of spring. However, some other regions show a considerable delay in the onset of spring over the study period, for example, the border area between China and Mongolia and in Qinghai-Tibet Plateau. The delay in the onset of spring has indeed been reported in this border area (Luo et al., 2021) and the southwestern Qinghai-Tibet Plateau (Shen et al., 2022). The reason is that in these areas the vegetation phenology is determined by the dynamics of both temperature and soil moisture (Luo et al., 2021; Shen et al., 2022). Moreover, the interannual fluctuation in the onset of spring shows a latitude-dependent development across the study area, with a smaller fluctuation at higher latitudes. Cold and polar (more continental) climates tend to have less interannual variation in vegetation phenology due to their generally regular interannual seasonality (Zhang et al., 2014). On the other hand, dry climate and seasonal dry tropical regions (e.g., South India) tend to have a higher interannual fluctuation in vegetation phenology due to a relatively more variable rainfall seasonality (Zhang et al., 2014).

Different species show different levels of integrity loss due to climate-induced heterogeneous shifts in vegetation phenology. Particularly those species with a relatively low migration network integrity, such as Chinese spot-billed duck, Baikal teal and falcated duck (*Mareca falcata*), are experiencing a higher level of integrity loss due to climate change. This might be because species with a stronger migration integrity tend to be more resilient to environmental change. Species wintering at relatively lower latitudes tend to experience a larger loss of integrity due to higher-level of heterogeneous shifts in vegetation phenology. The magnitude of phenology changes (Figures S5 and S9) and the interannual fluctuations (Figure S14) are both larger at lower latitudes than at higher ones. A greater difference in phenology shifts between two areas, as well as larger interannual fluctuations within areas, tend to lower the chance that bird arrival matches the peak abundance period of food, thereby reducing network integrity.

A decrease in between-node correlation strength of the onset of spring contributes most to the integrity loss of the migration network. The match–mismatch hypothesis states that the mismatch between food requirement and availability adversely effects consumer fitness (Cushing, 1990; Durant et al., 2007). While many migratory birds have advanced their migration in response to global warming (Beaumont et al., 2006; Jonzen, 2006), this response is generally considered insufficient in comparison to the rate of warming (Radchuk et al., 2019). Even though some goose species can advance their arrival further, they might not be able to accumulate sufficient energy during migration for egg-laying under these conditions (Lameris et al., 2018). Moreover, the situation would get worse when birds need to move to a next site with a shift in vegetation phenology out of sync from the current site.

Heterogeneous shifts in vegetation phenology deteriorate the migration network integrity, which might negatively affect energy intake, survival, and reproduction. We find that four species that are known to experience population decline (BirdLife International, 2022), i.e., Chinese spot-billed duck, swan goose, falcated duck (*Mareca falcata*), and bar-headed goose (*Anser indicus*), have a poorly connected migration network (the first two are also greatly affected by heterogeneous shifts in vegetation phenology). An increase of the population of the greater white-fronted goose (*Anser albifrons*) wintering in Japan and Korea, is generally recognized to reflect improved feeding conditions (Fox et al., 2005; Si et al., 2020), while the species is decreasing in China (Schmutz, 2018). Our study shows that the significant change trend (Figures S9–S11) and the interannual fluctuation of the onset of spring (Figures S14–S16) are both higher in China than in Japan and Korea, suggesting that heterogeneous shifts in vegetation phenology could be another crucial reason for the difference in population growth.

On the other hand, population trends (as well as migration network integrity) are affected by various external and internal factors, for example, habitat degradation and/or loss (Studds et al., 2017; Xu et al., 2019), the amount of climate change a species is experiencing, and the capacity in adapting to land cover and climate change. In addition to the amount of climate change a specific species is experiencing, a higher capacity in responding to climate change could mitigate certain level of integrity loss in the migration network. This could be further tested by future studies when new data (e.g., long-term survey data or satellite tracking data) become available for this region.

Our study has potential limitations that could be explored in future studies to improve the methodological framework. First, we use all predicted suitable areas as nodes in the migration network but not all areas are used in reality. This leads in general to a higher network integrity being detected for all species. On the other hand, in this way the effect of potential habitat could be considered in the calculation of network integrity. In addition, we generated a fixed buffer around each wetland to cover the potential foraging areas for all study species. In reality, the foraging distance would vary among species and among habitats. Using a species- and landscape-specific foraging distance would further improve the modelling of the suitable habitat. Second, we assume that the vegetation phenology metrics have an equally multiplicative effect on the movement probability. However, different species might respond differently to inter-and intra-annual shifts in vegetation phenology. In addition, birds might select foraging areas based on the current abundance of food, regardless of its phenological shifts and predictability.

Thirdly, our study only focuses on the impacts of the food phenology change in the migration network integrity. Moreover, peak food availability may be consistent across areas (nodes) or years, while the abundance is reduced (Kellermann & van Riper, 2015). Though onset of spring is critical, the heterogeneous shifts in the complete phenological curve, including peak, and senescence and offset could affect the level of the migration network connectivity change. Fourthly, species might consume foods that are not reflected in the vegetation phenology of an area such as seeds in farmland (Xu et al., 2024). Therefore, certain species-specific traits (e.g., wider dietary breath and higher foraging plasticity) could help mitigate integrity loss along the migration network to a certain extent. Besides food phenology, other cues might affect the migration phenology (e.g., photoperiod, temperature, snowmelt) and the effects may vary for different species (Newton, 2008). Therefore, the effect of food phenology change on the migration network integrity change might be overestimated if the effect of other cues on migration timing is stronger than food phenology.

This study proposes a novel approach that could be generally applied in different study systems to quantify the effect of the heterogeneous shifts in vegetation phenology, induced by climate change, on the migration network. Our approach could be integrated into climate change vulnerability assessments (CCVAs) to achieve a more accurate assessment of vulnerability under climate change for migratory species. CCVAs have frequently been used to measure the vulnerability of species posed by climate change, guiding management and conservation plans (Pacifici et al., 2015; Wheatley et al., 2017). The assessment is generally a combination of three aspects: exposure, sensitivity and adaptability, where exposure as the extrinsic factor is the magnitude of environmental change, sensitivity as the intrinsic factor is the tolerance of species to the change, and adaptability is the ability of species to adjust to the change (Pacifici et al., 2015). However, when choosing climate-related exposure, most studies only include the variation in temperature or precipitation over several years in the area that the target species occupies (Culp et al., 2017), overlooking the relationship among geographically distant areas used by migrants. Our framework systematically quantifies the exposure to climate change for migrants by taking the whole migration network into account, offers important information for the further assessment of migrant vulnerability under climate change, and is critical for identifying vulnerable species and regions for targeted conservation.

AUTHOR CONTRIBUTIONS

CONFLICT OF INTEREST STATEMENT

The authors declare no potential conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in Zenodo at https://doi.org/10.5281/zenodo.10429747.

ORCID

Jie Wei https://orcid.org/0000-0002-7280-2059

Fei Xu https://orcid.org/0009-0000-8020-2224

Ella F. Cole https://orcid.org/0000-0002-2689-946X

Ben C. Sheldon https://orcid.org/0000-0002-5240-7828

Willem F. de Boer https://orcid.org/0000-0003-3208-8521

Ben Wielstra https://orcid.org/0000-0002-7112-5965

Haohuan Fu https://orcid.org/0000-0002-6982-2235

Peng Gong https://orcid.org/0000-0003-1513-3765

Yali Si https://orcid.org/0000-0001-7107-9850

REFERENCES

Anderson, H. B., Godfrey, T. G., Woodin, S. J., & van der Wal, R. (2012). Finding food in a highly seasonal landscape: Where and how pink footed geese Anser brachyrhynchus forage during the Arctic spring. *Journal of Avian Biology*, 43(5), 415–422. https://doi.org/10.1111/j.1600-048X.2012.05699.x

Bauer, S., Van Dinther, M., Hogda, K.-A., Klaassen, M., & Madsen, J. (2008). The consequences of climate-driven stop-over sites changes on migration schedules and fitness of Arctic geese. *Journal of Animal Ecology*, 77(4), 654–660. https://doi.org/10.1111/j.1365-2656.2008.01381.x

Beaumont, L. J., McAllan, I. A. W., & Hughes, L. (2006). A matter of timing: Changes in the first date of arrival and last date of departure of Australian migratory birds. *Global Change Biology*, 12(7), 1339–1354. https://doi.org/10.1111/j.1365-2486.2006.01171.x

BirdLife International. (2022). IUCN Red List for birds. http://www.birdlife.org

BirdLife International and NatureServe. (2020). *Bird species distribution maps of the world version 5.0*. http://datazone.birdlife.org/species/requestdis

Cohen, J. M., Lajeunesse, M. J., & Rohr, J. R. (2018). A global synthesis of animal phenological responses to climate change. *Nature Climate Change*, 8(3), 224–228. https://doi.org/10.1038/s41558-018-0067-3

Culp, L. A., Cohen, E. B., Scarpignato, A. L., Thogmartin, W. E., & Marra, P. P. (2017). Full annual cycle climate change vulnerability assessment for migratory birds. *Ecosphere*, 8(3), e01565. https://doi.org/10.1002/ecs2.1565

Cushing, D. H. (1990). Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. *Advances in Marine Biology*, 26, 249–293. https://doi.org/10.1016/s0065-2881(08)60202-3

Danielson, J. J., & Gesch, D. B. (2011). Global multi-resolution terrain elevation data 2010 (GMTED2010): U.S. Geological Survey open-file report 2011–1073. 26.

Drent, R. H., Fox, A. D., & Stahl, J. (2006). Travelling to breed. *Journal of Ornithology*, 147(2), 122–134. https://doi.org/10.1007/s10336-006-0066-4

Durant, J. M., Hjermann, D. O., Ottersen, G., & Stenseth, N. C. (2007). Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, 33(3), 271–283. https://doi.org/10.3354/cr033271

Duriez, O., Bauer, S., Destin, A., Madsen, J., Nolet, B. A., Stillman, R. A., & Klaassen, M. (2009). What decision rules might pink-footed geese use to depart on migration? An individual-based model. *Behavioral Ecology*, 20(3), 560–569. https://doi.org/10.1093/beheco/arp032

Eklundh, L., & Jönsson, P. (2015). *TIMESAT 3.2 software manual*. Lund and Malmö University.

Emmenegger, T., Hahn, S., Arlettaz, R., Amrhein, V., Zehtindjiev, P., & Bauer, S. (2016). Shifts in vegetation phenology along flyways entail varying risks of mistiming in a migratory songbird. *Ecosphere*, 7(6), e01385. https://doi.org/10.1002/ecs2.1385

European Centre. (2020). *C3S product user guide and specification (PUGS) - ICDR land cover 2016 to 2019*. https://datastore.copernicus-climate.eu/documents/satellite-land-cover/D3.3.12-v1.3_PUGS_ICDR_LC_v2.1.x_PRODUCTS_v1.3.pdf

European Space Agency. (2017). *Land cover CCI product user guide version 2*. http://maps.elie.ucl.ac.be/CCI/viewer/download/ESACCI-LC-Ph2-PUGv2_2.0.pdf

Fang, B., Yang, Z. Y., Shen, M. G., Wu, X. X., & Hu, J. H. (2021). Limited increase in asynchrony between the onset of spring green-up and the arrival of a long-distance migratory bird. *Science of the Total Environment*, 795, 9. https://doi.org/10.1016/j.scitotenv.2021.148823

Fox, A. D., Madsen, J., Boyd, H., Kuijken, E., Norriss, D. W., Tombre, I. M., & Stroud, D. A. (2005). Effects of agricultural change on abundance, fitness components and distribution of two Arctic-nesting goose populations. *Global Change Biology*, 11(6), 881–893. https://doi.org/10.1111/j.1365-2486.2005.00941.x

Gilroy, J. J., Gill, J. A., Butchart, S. H. M., Jones, V. R., & Franco, A. M. A. (2016). Migratory diversity predicts population declines in birds. *Ecology Letters*, 19(3), 308–317. https://doi.org/10.1111/ele.12569

Jeong, S. J., Ho, C. H., Gim, H. J., & Brown, M. E. (2011). Phenology shifts at start vs. end of growing season in temperate vegetation over the Northern Hemisphere for the period 1982–2008. *Global Change Biology*, 17(7), 2385–2399. https://doi.org/10.1111/j.1365-2486.2011.02397.x

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, 491(7424), 444–448. https://doi.org/10.1038/nature11631

Jiang, Z., Huete, A. R., Didan, K., & Miura, T. (2008). Development of a two-band enhanced vegetation index without a blue band. *Remote Sensing of Environment*, 112(10), 3833–3845. https://doi.org/10.1016/j.rse.2008.06.006

Johansson, J., Kristensen, N. P., Nilsson, J. A., & Jonzen, N. (2015). The eco-evolutionary consequences of interspecific phenological asynchrony - a theoretical perspective. *Oikos*, 124(1), 102–112. https://doi.org/10.1111/oik.01909

Johnston, A., Hochachka, W. M., Strimas-Mackey, M. E., Ruiz Gutierrez, V., Robinson, O. J., Miller, E. T., Auer, T., Kelling, S. T., & Fink, D. (2021). Analytical guidelines to increase the value of community science data: An example using eBird data to estimate species distributions. *Diversity and Distributions*, 27(7), 1265–1277. https://doi.org/10.1111/ddi.13271

Jönsson, P., & Eklundh, L. (2002). Seasonality extraction by function fitting to time-series of satellite sensor data. *IEEE Transactions of Geoscience and Remote Sensing*, 40(8), 1824–1832. https://doi.org/10.1109/TGRS.2002.802519

Jönsson, P., & Eklundh, L. (2004). TIMESAT—A program for analyzing time-series of satellite sensor data. *Computers & Geosciences*, 30(8), 833–845. https://doi.org/10.1016/j.cageo.2004.05.006

Jonzen, N. (2006). Rapid advance of spring arrival dates in long-distance migratory birds. *Science*, 312(5782), 1959–1961. https://doi.org/10.1126/science.1126119

Kellermann, J. L., & van Riper, C. (2015). Detecting mismatches of bird migration stopover and tree phenology in response to changing climate. *Oecologia*, 178(4), 1227–1238. https://doi.org/10.1007/s00442-015-3293-7

Kharouba, H. M., Ehrlen, J., Gelman, A., et al. (2018). Global shifts in the phenological synchrony of species interactions over recent decades. *Proceedings of the National Academy of Sciences of the United States of America*, 115(20), 5211–5216. https://doi.org/10.1073/pnas.1714511115

Knudsen, E., Linden, A., Both, C., Jonzen, N., Pulido, F., Saino, N., Sutherland, W. J., Bach, L. A., Coppack, T., Ergon, T., Gienapp, P., Gill, J. A., Gordo, O., Hedenstrom, A., Lehikoinen, E., Marra, P. P., Moller, A. P., Nilsson, A. L. K., Peron, G., … Stenseth, N. C. (2011). Challenging claims in the study of migratory birds and climate change. *Biological Reviews*, 86(4), 928–946. https://doi.org/10.1111/j.1469-185X.2011.00179.x

Kolzsch, A., Bauer, S., de Boer, R., Griffin, L., Cabot, D., Exo, K. M., van der Jeugd, H. P., & Nolet, B. A. (2015). Forecasting spring from afar? Timing of migration and predictability of phenology along different migration routes of an avian herbivore. *Journal of Animal Ecology*, 84(1), 272–283. https://doi.org/10.1111/1365-2656.12281

La Sorte, F. A., Lepczyk, C. A., Burnett, J. L., Hurlbert, A. H., Tingley, M. W., & Zuckerberg, B. (2018). Opportunities and challenges for big data ornithology. *The Condor*, 120(2), 414–426. https://doi.org/10.1650/condor-17-206.1

Lameris, T. K., van der Jeugd, H. P., Eichhorn, G., Dokter, A. M., Bouten, W., Boom, M. P., Litvin, K. E., Ens, B. J., & Nolet, B. A. (2018). Arctic geese tune migration to a warming climate but still suffer from a phenological mismatch. *Current Biology*, 28(15), 2467–2473. https://doi.org/10.1016/j.cub.2018.05.077

Lehner, B., & Doll, P. (2004). Development and validation of a global database of lakes, reservoirs and wetlands. *Journal of Hydrology*, 296(1–4), 1–22. https://doi.org/10.1016/j.jhydrol.2004.03.028

Luo, M., Meng, F. H., Sa, C. L., Duan, Y. C., Bao, Y. H., Liu, T., & De Maeyer, P. (2021). Response of vegetation phenology to soil moisture dynamics in the Mongolian Plateau. *Catena*, 206, 105505. https://doi.org/10.1016/j.catena.2021.105505

Marra, P. P., Cohen, E. B., Loss, S. R., Rutter, J. E., & Tonra, C. M. (2015). A call for full annual cycle research in animal ecology. *Biology Letters*, 11(8), 4. https://doi.org/10.1098/rsbl.2015.0552

Mayor, S. J., Guralnick, R. P., Tingley, M. W., Otegui, J., Withey, J. C., Elmendorf, S. C., Andrew, M. E., Leyk, S., Pearse, I. S., & Schneider, D. C. (2017). Increasing phenological asynchrony between spring green-up and arrival of migratory birds. *Scientific Reports*, 7(1), 1902. https://doi.org/10.1038/s41598-017-02045-z

Miller-Rushing, A. J., Hoye, T. T., Inouye, D. W., & Post, E. (2010). The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1555), 3177–3186. https://doi.org/10.1098/rstb.2010.0148

Mundkur, T. (2006). Successes and challenges of promoting conservation of migratory waterbirds and wetlands in the Asia-Pacific region: Nine years of a regional strategy. In G. C. Boere, C. A. Galbraith, & D. A. Stroud (Eds.), *Waterbirds around the world* (pp. 81–87). The Stationery Office.

Newton, I. (2008). *The migration ecology of birds*. Elsevier Ltd.

Pacifici, M., Foden, W. B., Visconti, P., Watson, J. E. M., Butchart, S. H. M., Kovacs, K. M., Scheffers, B. R., Hole, D. G., Martin, T. G., Akçakaya, H. R., Corlett, R. T., Huntley, B., Bickford, D., Carr, J. A., Hoffmann, A. A., Midgley, G. F., Pearce-Kelly, P., Pearson, R. G., Williams, S. E., … Rondinini, C. (2015). Assessing species vulnerability to climate change. *Nature Climate Change*, 5(3), 215–225. https://doi.org/10.1038/nclimate2448

Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, 401(6756), 877–884. https://doi.org/10.1038/44766

Piao, S. L., Liu, Q., Chen, A. P., Janssens, I. A., Fu, Y. S., Dai, J. H., Liu, L. L., Lian, X., Shen, M. G., & Zhu, X. L. (2019). Plant phenology and global climate change: Current progresses and challenges. *Global Change Biology*, 25(6), 1922–1940. https://doi.org/10.1111/gcb.14619

R Core Team. (2021). *R: A language and environment for statistical computing*. Austria. https://www.R-project.org/

Radchuk, V., Reed, T., Teplitsky, C., van de Pol, M., Charmantier, A., Hassall, C., Adamík, P., Adriaensen, F., Ahola, M. P., Arcese, P., Miguel Avilés, J., Balbontin, J., Berg, K. S., Borras, A., Burthe, S., Clobert, J., Dehnhard, N., de Lope, F., Dhondt, A. A., … Kramer-Schadt, S. (2019). Adaptive responses of animals to climate change are most likely insufficient. *Nature Communications*, 10(1), 3109. https://doi.org/10.1038/s41467-019-10924-4

Reed, B. C., & Ohlen, D. O. (1994). Measuring phenological variability from satellite imagery. *Journal of Vegetation Science*, 5(5), 703–714. https://doi.org/10.2307/3235884

Samplonius, J. M., Atkinson, A., Hassall, C., Keogan, K., Thackeray, S. J., Assmann, J. J., Burgess, M. D., Johansson, J., Macphie, K. H., Pearce-Higgins, J. W., Simmonds, E. G., Varpe, Ø., Weir, J. C., Childs, D. Z., Cole, E. F., Daunt, F., Hart, T., Lewis, O. T., Pettorelli, N., … Phillimore, A. B. (2021). Strengthening the evidence base for temperature-mediated phenological asynchrony and its impacts. *Nature Ecology & Evolution*, 5(2), 155–164. https://doi.org/10.1038/s41559-020-01357-0

Saura, S., Estreguil, C., Mouton, C., & Rodríguez-Freire, M. (2011). Network analysis to assess landscape connectivity trends: Application to European forests (1990–2000). *Ecological Indicators*, 11(2), 407–416. https://doi.org/10.1016/j.ecolind.2010.06.011

Saura, S., & Torné, J. (2009). Conefor Sensinode 2.2: A software package for quantifying the importance of habitat patches for landscape connectivity. *Environmental Modelling & Software*, 24(1), 135–139. https://doi.org/10.1016/j.envsoft.2008.05.005

Schmutz, J. A. (2018). *A global audit of the status and trends of Arctic and Northern Hemisphere goose populations*. https://pubs.usgs.gov/publication/70196227

Shen, M., Wang, S., Jiang, N., Sun, J., Cao, R., Ling, X., Fang, B., Zhang, L., Zhang, L., Xu, X., Lv, W., Li, B., Sun, Q., Meng, F., Jiang, Y., Dorji, T., Fu, Y., Iler, A., Vitasse, Y., … Fu, B. (2022). Plant phenology changes and drivers on the Qinghai–Tibetan Plateau. *Nature Reviews Earth and Environment*, 3(10), 633–651. https://doi.org/10.1038/s43017-022-00317-5

Si, Y., Wei, J., Wu, W., Zhang, W., Hou, L., Yu, L., & Wielstra, B. (2020). Reducing human pressure on farmland could rescue China's declining wintering geese. *Movement Ecology*, 8(1), 35. https://doi.org/10.1186/s40462-020-00220-y

Si, Y., Xu, Y., Xu, F., Li, X., Zhang, W., Wielstra, B., Wei, J., Liu, G., Luo, H., Takekawa, J., Balachandran, S., Zhang, T., de Boer, W. F., Prins, H. H. T., & Gong, P. (2018). Spring migration patterns, habitat use, and stopover site protection status for two declining waterfowl species wintering in China as revealed by satellite tracking. *Ecology and Evolution*, 8(12), 6280–6289. https://doi.org/10.1002/ece3.4174

Studds, C. E., Kendall, B. E., Murray, N. J., Wilson, H. B., Rogers, D. I., Clemens, R. S., Gosbell, K., Hassell, C. J., Jessop, R., Melville, D. S., Milton, D. A., Minton, C. D. T., Possingham, H. P., Riegen, A. C., Straw, P., Woehler, E. J., & Fuller, R. A. (2017). Rapid population decline in migratory shorebirds relying on Yellow Sea tidal mudflats as stopover sites. *Nature Communications*, 8, 14895. https://doi.org/10.1038/ncomms14895

Sullivan, B. L., Aycrigg, J. L., Barry, J. H., Bonney, R. E., Bruns, N., Cooper, C. B., Damoulas, T., Dhondt, A. A., Dietterich, T., Farnsworth, A., Fink, D., Fitzpatrick, J. W., Fredericks, T., Gerbracht, J., Gomes, C., Hochachka, W. M., Iliff, M. J., Lagoze, C., la Sorte, F. A., … Kelling, S. (2014). The eBird enterprise: An integrated approach

to development and application of citizen science. *Biological Conservation*, *169*, 31–40. https://doi.org/10.1016/j.biocon.2013.11.003

Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., Helaouet, P., Johns, D. G., Jones, I. D., Leech, D. I., Mackay, E. B., Massimino, D., Atkinson, S., Bacon, P. J., Brereton, T. M., Carvalho, L., Clutton-Brock, T. H., Duck, C., Edwards, M., … Wanless, S. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, *535*(7611), 241–U294. https://doi.org/10.1038/nature18608

The MathWorks Inc. (2022). *MATLAB version: 9.12.0 (R2022a)*. The MathWorks Inc. https://www.mathworks.com

Tombre, I. M., Hogda, K. A., Madsen, J., Griffin, L. R., Kuijken, E., Shimmings, P., Rees, E., & Verscheure, C. (2008). The onset of spring and timing of migration in two arctic nesting goose populations: The pink-footed goose *Anser bachyrhynchus* and the barnacle goose *Branta leucopsis*. *Journal of Avian Biology*, *39*(6), 691–703. https://doi.org/10.1111/j.1600-048X.2008.04440.x

Urban, D., & Keitt, T. (2001). Landscape connectivity: A graph-theoretic perspective. *Ecology*, *82*(5), 1205–1218. https://doi.org/10.2307/2679983

Vermote, E. F., Roger, J. C., & Ray, J. P. (2015). *MODIS surface reflectance user's guide, collection 6*. http://modis-sr.ltdri.org

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, *416*(6879), 389–395. https://doi.org/10.1038/416389a

Wei, J., Xin, Q. C., Ji, L. Y., Gong, P., & Si, Y. L. (2019). A new satellite-based indicator to identify spatiotemporal foraging areas for herbivorous waterfowl. *Ecological Indicators*, *99*, 83–90. https://doi.org/10.1016/j.ecolind.2018.12.016

Wetlands International. (2012). *Waterbird population estimates, fifth edition. Summary report*. Wetlands International.

Wheatley, C. J., Beale, C. M., Bradbury, R. B., Pearce-Higgins, J. W., Critchlow, R., & Thomas, C. D. (2017). Climate change vulnerability for species-assessing the assessments. *Global Change Biology*, *23*(9), 3704–3715. https://doi.org/10.1111/gcb.13759

Wilman, H., Belmaker, J., Simpson, J., et al. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, *95*(7), 2027. https://doi.org/10.1890/13-1917.1

Xu, F., Wu, W., Wei, J., Xin, Q., Wielstra, B., La Sorte, F. A., Ma, Z., Lei, G., Lei, J., Wu, W., Yang, Y., Gong, P., Xu, B., & Si, Y. (2024). Migratory

herbivorous waterfowl track multiple resource waves during spring migration. *bioRxiv*, 2023.2004.2014.536842. https://doi.org/10.1101/2023.04.14.536842

Xu, Y., Si, Y., Wang, Y., Zhang, Y., Prins, H. H. T., Cao, L., & de Boer, W. F. (2019). Loss of functional connectivity in migration networks induces population decline in migratory birds. *Ecological Applications*, *29*(7), e01960. https://doi.org/10.1002/eap.1960

Youngflesh, C., Montgomery, G. A., Saracco, J. F., Miller, D. A. W., Guralnick, R. P., Hurlbert, A. H., Siegel, R. B., LaFrance, R., & Tingley, M. W. (2023). Demographic consequences of phenological asynchrony for North American songbirds. *Proceedings of the National Academy of Sciences of the United States of America*, *120*(28), e2221961120. https://doi.org/10.1073/pnas.2221961120

Youngflesh, C., Socolar, J., Amaral, B. R., Arab, A., Guralnick, R. P., Hurlbert, A. H., LaFrance, R., Mayor, S. J., Miller, D. A. W., & Tingley, M. W. (2021). Migratory strategy drives species-level variation in bird sensitivity to vegetation green-up. *Nature Ecology & Evolution*, *5*, 987–994. https://doi.org/10.1038/s41559-021-01442-y

Zhang, X., Tan, B., & Yu, Y. (2014). Interannual variations and trends in global land surface phenology derived from enhanced vegetation index during 1982–2010. *International Journal of Biometeorology*, *58*(4), 547–564. https://doi.org/10.1007/s00484-014-0802-z

SUPPORTING INFORMATION

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

How to cite this article: Wei, J., Xu, F., Cole, E. F., Sheldon, B. C., de Boer, W. F., Wielstra, B., Fu, H., Gong, P., & Si, Y. (2024). Spatially heterogeneous shifts in vegetation phenology induced by climate change threaten the integrity of the avian migration network. *Global Change Biology*, *30*, e17148. https://doi.org/10.1111/gcb.17148