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RESEARCH ARTICLE

Species-dependent effects of habitat degradation in relation to seasonal distribution of migratory waterfowl in the East Asian–Australasian Flyway

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Abstract

Context Migratory species' resilience to landscape changes depends on spatial patterns of habitat degradation in relation to their migratory movements, such as the distance between breeding and non-breeding areas, and the location and width of migration corridors.

Objectives We investigated to what extent the impact of habitat degradation depended on the seasonal distributions of migratory waterfowl.

Methods Using logistic regression, we selected wetland sites for eight waterfowl species in the East Asian–Australasian Flyway (EAAF) by calculating the probabilities of species occurrence per wetland site in relation to environmental factors. We quantified landscape metrics related to habitat degradation within these wetland sites. We used general linear models to test for differences in the effects of habitat degradation on waterfowl species with different migration extents and at different latitudes.

Results The patterns of habitat degradation differed spatially across the EAAF and affected species to a different degree. Species with shorter and broader migration corridors (*Anser cygnoid* and *A. anser*) could benefit from improved habitat conditions in the west of the EAAF. Species with longer and narrower migration corridors (*Cygnus columbianus*, *A. fabalis*, *A. albifrons*, *A. erythropus*, *Anas crecca*, and *Anas acuta*) were under higher risk of habitat degradation in the coastal regions of China and Japan.

Conclusions Migratory species with longer and narrower migration corridors are more affected by habitat degradation, because they might have fewer

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alternative stopover sites at similar latitude. Our findings improve the understanding of species-specific effects of environmental changes on migratory species, and defines critical and endangered wetland sites, and vulnerable species.

Keywords Seasonal distribution · Species trait · Migratory waterfowl · Habitat loss · Fragmentation · Isolation · East Asian–Australasian Flyway · Migratory connectivity · Wetland

Introduction

Habitat loss is one of the most important factors causing population declines in migratory birds (Sanderson et al. 2006). Habitat degradation along migration routes has been linked to decreases in populations of a number of migratory bird populations (Iwamura et al. 2013; Studds et al. 2017). Wetlands, the main habitat for migratory waterfowl species, are among the most threatened habitats worldwide, and nearly half of the world's wetlands have disappeared as a result of the expansion of human activities (Millennium Ecosystem Assessment 2005; Silva et al. 2007). China has lost 33% of its wetland area from 1978 to 2008, although the trend of wetland loss is slowing down lately (Niu et al. 2012). Hence, in the last decades, ecosystem service values of natural areas have declined substantially as a consequence of wetland loss and degradation (Wang et al. 2006).

Landscape composition and configuration of suitable habitats affect species occurrence and richness (Guadagnin and Maltchik 2007; Mora et al. 2011; Xu et al. 2014; Zhang et al. 2018). Availability of wetlands and waterbodies, wetland size, and wetland connectivity positively influence waterfowl species occurrence and species richness, while wetlands in proximity to rice fields, total rice field area, and wetland isolation have negative effects (Guadagnin and Maltchik 2007; Zhang et al. 2018). Therefore, waterfowl habitat degradation can be quantified by land cover changes and dynamics in landscape variables of wetland sites along migration corridors (Van Eerden et al. 2005; Tian et al. 2008). However, because of limited attention to the spatio-temporal dynamics of wetland sites along migration routes (Dong et al. 2015), it is currently unknown how current trends of habitat degradation influence migratory waterfowl species.

The East Asian–Australasian Flyway is one of the nine major waterbird flyways globally. The flyway holds over 50 million migratory waterbirds, including 51 threatened or near-threatened species (EAAFP 2017). Because of the loss and degradation of suitable habitats, resulting from rapid economic development and human disturbance, population sizes for many waterfowl species in the northern part of the flyway have declined rapidly (Syroechkovskiy 2006; Cao et al. 2008, 2010; de Boer et al. 2011; Si et al. 2018).

The delineated range of the East Asian–Australasian Flyway is rather broad, so the species that use it display considerable variability in the spatial patterns of their breeding, non-breeding, and stopover sites. For instance, the swan goose (*Anser cygnoid*) breeds in both eastern and western Mongolia (Batbayar et al. 2013), while the greater white-fronted goose (*Anser albifrons*) is an Arctic-breeding migrant with a distribution extending to the Lena Delta, Siberia. However, the non-breeding grounds of the greater white-fronted goose in the Yangtze River Basin overlap with those of swan goose (Si et al. 2018). The falcated duck (*Mareca falcata*) uses both the eastern and central parts of the East Asian–Australasian Flyway, while the common teal (*Anas crecca*) is restricted to the eastern part of the flyway (Takekawa et al. 2010).

The spatial extent of these waterfowl species' seasonal distributions probably influences the degree to which they are affected by habitat degradation. For instance, population sizes of long-distance migratory species decline more rapidly than those of short-distance migratory species (Morrison et al. 2013). Independently of the distance of migration, species with broader dispersal ranges are less prone to population declines compared to those whose ranges are restricted, because of spatial variation in habitat degradation (Gilroy et al. 2016). In addition, the underlying patterns of habitat loss also make a difference in species-specific consequences of habitat degradations, e.g., a small amount of habitat loss in certain crucial stopover sites can trigger severe impacts (Weber et al. 1999; Runge et al. 2014). The resilience of waterfowl species to environmental changes varies because of spatial patterns in habitat degradation and differences in the species' seasonal distributions. However, habitat degradation has not been analysed for its species-specific effects as a consequence of the spatial variation in migration patterns.

In this study, we quantified the spatial patterns of habitat degradation in wetland sites, in relation to the seasonal distributions of eight waterfowl species. Wetland sites can be located in breeding grounds, non-breeding grounds, or stopover sites in a species' migration route. First, we selected all wetland sites where each species was likely to occur in the distribution ranges of each waterfowl species based on the modelled relationships between species occurrence and environmental factors (hereafter suitable wetland sites). Second, within the ranges of suitable wetland sites, as metrics of habitat degradation, we quantified the availability of water area, grassland, and wetland, and quantified wetland fragmentation and isolation, and changes in agricultural resources. Finally, we explored the species-specific effects of habitat degradation in relation to the species' migratory extents. The risk from habitat degradation is determined by how the species' distribution overlaps with the spatial distribution of habitat changes. We expect that migratory species with a longer and narrower migration corridors are more likely to be affected by habitat degradation. The results can provide a better understanding of the underlying mechanisms of how environmental changes affect different migratory species, so that targeted conservation plans can be developed for critical and endangered wetland sites and vulnerable species.

Methods

Study area

The East Asian–Australasian Flyway identified by the global monitoring program of Wetland International stretches across 22 countries, covering East Asia, Southeast Asia, Australia, and New Zealand, and northern areas from the Taimyr Peninsula in Russia to Alaska (EAAFP 2017). Unlike Artic-breeding shorebirds that spend the non-breeding season in Australia and New Zealand, most of the Arctic-breeding waterfowl in the East Asian–Australasian Flyway migrate only as far south as China (Birdlife International and NatureServe 2015). We focused on the waterfowl populations overwintering in the Yangtze River Basin, one of the most important non-breeding grounds in the flyway. Therefore, the study area extended from the Yangtze River Basin to the northern part of the East Asian–Australasian Flyway (Appendix S1). Overall, the study area overlaps with six countries: China, Mongolia, North Korea, South Korea, Japan, and Russia.

Study species

The wetlands in the Yangtze River Basin are key non-breeding sites of eleven goose, swan, and dabbling duck species (Cao et al. 2010), including tundra swan (*Cygnus columbianus*), swan goose, bean goose (*Anser fabalis*), greater white-fronted goose, lesser white-fronted goose (*Anser erythropus*), greylag goose (*Anser anser*), falcated duck, Baikal teal (*Sibirionetta formosa*), common teal, spot-billed duck (*Anas poecilorhyncha*), and northern pintail (*Anas acuta*). Eight of the eleven species were included in our analysis. Falcated duck, Baikal teal, and spot-billed duck were excluded because of a lack of detailed information about their breeding distribution (Birdlife International and NatureServe 2015).

Data

Bird data

Breeding and non-breeding ranges of the eight waterfowl species were obtained from bird species distribution maps of the world (v5.0), produced by Birdlife International (Birdlife International and NatureServe 2015). Information on the occurrence of the eight Anatidae species within the study area was obtained from the eBird citizen-science database: eBird Basic Dataset (v1.5), which provides species scientific name, population count, latitude, longitude, and date and time of bird observations (Sullivan et al. 2014; Cornell Lab of Ornithology 2016). All records from 1992 to 2016 were included in the analysis, except for data that were not verified by eBird editors. Duplicate records of the same species, location, date, and time of observations were excluded. The records of the eight study species with in the study area were included in the analysis. In total, there were 89 locations with observations of greylag goose, 197 for swan goose, 173 for bean goose, 357 for greater white-fronted goose, 57 for lesser white-fronted goose, 223 for tundra swan, 408 for common teal, and 1110 for northern pintail within the study area.

Data for environmental factors

The polygons of lakes, reservoirs, and smaller water bodies (called ‘wetland sites’ here) with a surface area $\geq$ 0.1 km^2 were obtained from the Global Lakes and Wetlands Database (GLWD-1 and GLWD-2; accessed on 22-02-2017; (Lehner and Döll 2004). The 500-m-resolution elevation data was obtained from Jonathan de Ferranti’s Digital Elevation Data site (accessed on 07-03-2017), which combines data from multiple sources, including ASTER Global Digital Elevation Map (ASTER GDEM), gap-filling Shuttle Radar Topography Mission (known as SRTM), and contour maps (de Ferranti 2014). The area of food resources (grassland and cropland) around each lake was derived from the ESA CCI 300-m global land cover products (v2.0.7) of the year 1992 (European Space Agency 2017).

Land cover data for landscape metrics

We used land cover maps for 1992 and 2012 from the European Space Agency (ESA) CCI 300-m annual global land cover products (European Space Agency 2017) to quantify the spatial patterns of habitat degradation. The land cover was reclassified into six types: water (water bodies), woodland (tree cover and shrubland), grassland (herbaceous cover, grasslands, and lichens and mosses), cropland (agricultural crops), bareland (bare areas, sparse herbaceous cover, unconsolidated bare areas, and permanent snow and ice), and urban and built-up areas (urban areas and consolidated bare areas). The croplands north of the Amur were not included in the analysis for two reasons. First, there are few croplands in those regions because of an unsuitable climate and low human density. Second, small patches of croplands could scarcely be detected by the 300-m-resolution remote sensing devices, and the clear-cuts created by logging activities and forest fires, a widespread event in Siberian forests, can be misclassified as cropland.

Identification of suitable wetland sites

The selection of suitable wetland sites in the distribution ranges of each study species was achieved by calculating the probabilities of species occurrence in relation to environmental factors. We assumed that the migratory birds do not travel further north than their breeding ranges or further south than their non-breeding ranges. Therefore, for each species, we first selected all wetlands that fell within the study area (Appendix S1) as well as between their northernmost extent of the breeding range and southernmost extent of their non-breeding range (Birdlife International and NatureServe 2015). Habitat selection by migratory waterfowl is mainly based on availability and suitability of wetlands and influenced by the type and extent of surrounding land-use types (Davis et al. 2014). Therefore, we built a logistic regression model using the presence/absence of a study species in each wetland, in relation to lake area (km^2), elevation (m), x coordinates (m; to represent the East–West gradient under the azimuthal equidistant projection) of lakes, and surrounding extent of suitable foraging areas, to predict the suitable wetland sites for each study species. Lakes with one or more observations of a study species were defined as presence records. We then randomly generated an equal number of absence records in the lakes where ebirder visited but without observations of the specific study species. Distances between roosting and foraging sites of waterfowl species in general do not exceed their maximum foraging flight distance (Beatty et al. 2014), so the surrounding extent of foraging areas was measured by the area (km^2) of grassland and cropland within a 32.5-km radius buffer around each lake, which is the maximum mean foraging flight distances of ducks and geese (Johnson et al. 2014). Both x coordinates, as measured by the center x coordinate of each lake, and the squared x coordinate, were added to the model because we assumed a dome-shaped relationship between the chance of a wetland being used by a specific species and the x-coordinate, for example, higher near the coast or higher in the center of their migration extent than at the edge.

For each species, the best model with the smallest bias-adjusted Akaike’s information criterion was selected (Burnham and Anderson 2003). By classifying the predicted probability of occurrence as presence or absence with a cutoff value of 50%, the accuracy of the models was calculated by summing the number of true positive cases (classified by the model as presence and the species is present in reality) and true negatives (classified by the model as absence and the species is absent in reality) divided by total number of cases (Olson and Delen 2008). A wetland site was defined as suitable when the predicted probability of presence of the specific species exceeded 50% (Appendix S3). The wetland area in subsequent analyses included these suitable lakes and a 32.5-km buffer around each of these suitable lakes (Olson and Delen 2008).

All distances and coordinates were calculated under the azimuthal equidistant projection, and all areas were calculated under the cylindrical equal area. Calculations of the environmental factors were performed in ArcMap 10.2.1 (ESRI, San Diego, CA, USA). Logistic regressions were performed with package 'lme4' (Bates et al. 2014), and model selections were performed with package 'MuMIn'(Burnham and Anderson 2003) in R 3.3.3.

Quantification of habitat degradation

To quantify how habitats in these suitable wetland sites changed from 1992 to 2012, we calculated six landscape metrics including availability of water area, grassland, and wetland, and quantified wetland fragmentation and isolation, and changes in agriculture resources in 1992 and 2012, respectively (Table 1). Water and surrounding grasslands were aggregated into wetland properties, as both the area of open water and surrounding grasslands affect the suitability of a wetland for waterfowl (Horn et al. 2005; Beatty et al. 2014). The size of a wetland is a key predictor for waterfowl species richness, and wetland connectivity and isolation are additional landscape metrics affecting waterfowl habitat quality (Guadagnin and Maltchik 2007; Zhang et al. 2015).

All landscape metrics were measured per suitable wetland site in each 100 × 100 km grid cell, as the upper quartile of scales at which habitat configuration affects the distribution of species is approximately 100 km, partly because the maximum radius of a species' foraging flight is generally smaller than 50 km (Ackerman et al. 2006; McGill 2010; Si et al. 2011; Johnson et al. 2014). Water, grassland, and wetland availability were measured by the total area of water bodies, grassland, and wetlands, respectively. Wetland fragmentation was measured by the change in mean patch area of wetlands. Wetland isolation was quantified by the change in the Proximity Index, which equals the sum of the wetland patch area divided by the squared edge-to-edge distance between a wetland patch and the wetland patches whose edges are within 32.5 km around the specific patch (Gustafson and Parker 1992), as:

$$\textit{Proximity index} = \sum_{s=1}^{n} \frac{a_{ijs}}{d_{ijs}^2}$$

where n equals number of wetland patches within the suitable wetland sites in each 200 × 200 km grid cell; a_{ijs} is the area of wetland patch ij, which is within in a distance of 32.5 km around focal wetland patch s; d_{ijs} is the edge-to-edge distance between wetland patch ij and focal wetland patch s. The availability of agricultural resources was quantified by the total area of cropland.

All calculations were conducted under the azimuthal equidistant projection. Geographic data for calculating landscape metrics were prepared with ArcMap 10.2.1 (ESRI, San Diego, CA, USA). Fragstats 4.2 (McGarigal and Marks 1995) was used to calculate landscape metrics.

Exploration of species variation affected by habitat degradation

Habitat degradation was quantified by the change ratios of the six landscape metrics from 1992 to 2012 in each 100 × 100 km grid cell, as:

$$\textit{Change ratio} = \ln\left(\frac{V_{2012}}{V_{1992}}\right)$$

where V_{1992} and V_{2012} is the value of each landscape metric in 1992 and 2012, respectively. To better understand the latitudinal, national, and species-specific patterns of habitat degradation, the mean change ratio of each landscape metric in each 5-degree latitudinal zone (each zone is 5-degree wide), each country, and in each breeding, non-breeding, and stopover area (the suitable wetland sites in between their breeding and non-breeding ranges) of each study species was calculated by overlapping the species' ranges with the calculated six landscape metrics maps (grid cell: 100 × 100 km).

Three general linear models (GLMs) were applied to test (1) whether patterns of wetland degradation

Table 1 Landscape variables associated with waterfowl habitat degradation

Variable	Index for	Description
Total area (ha)	Wetland availability	Wetland size
Mean area (ha)	Wetland Fragmentation	The average wetland patch area
Proximity Index	Wetland Isolation	A measurement of relative isolation of the wetland patches. High value indicates habitat patches are connected to each other within a buffer distance, while low Proximity Index value indicates they are isolated from each other (Gustafson and Parker 1992)
Total water area (ha)	Water area availability	A measurement of availability of water surface as roosting habitats
Total grassland area (ha)	Grassland availability	A measurement of availability of grasslands as primary food resources
Total crop area (ha)	Agriculture Resources	A measurement of availability of croplands as additional food resources

All landscape metrics were measured in the suitable wetland sites in each 100 × 100 km grid cell. Wetland properties include water and surrounding grassland. The changes were quantified by change ratios from 1992 to 2012

change over latitude and (2) whether the patterns differs among species with different migration extent (i.e., species with shorter and broader migration corridors versus those with longer and narrower migration corridors). The three dependent variables were the mean of absolute changes in the change ratios of wetland availability, fragmentation, and isolation, respectively. Independent variables of each model included one continuous variable (latitude) and one categorical variable (the species catalogue with two classes; i.e., '1' is species with longer and narrower migration corridors; '2' is species with shorter and broader migration corridors). We defined six out of the eight study species (tundra swan, bean goose, greater white-fronted goose, lesser white-fronted goose, common teal, and northern pintail) as species with longer and narrower migration corridors, with their seasonal distribution extending from the Lower Yangtze to Siberia. The swan goose and greylag goose were classified as species with shorter and broader migration corridors that breed in Mongolian regions and occupy more western parts of the flyway compared to the first group of species (Fig. 1). This classification is in agreement with previous findings (Morrison et al. 2013; Gilroy et al. 2016).

The changes in landscape variables in different regions was calculated with ArcMap 10.2.1. The basic statistics were calculated in R 3.3.3, and the GLMs were carried out with package 'lme4' (Bates et al. 2014) in R 3.3.3.

Results

Environmental factors and the presence of waterfowl in wetland sites

According to the best models, the presence of all goose and duck species was positively related to area of lakes, and the presence of all species (except lesser white-fronted goose) was positively related to surrounding food resources (i.e., grass and crop resources; Table 2). The probability of presence for greater white-fronted goose, lesser white-fronted goose, tundra swan, and northern pintail increased with decreasing elevation (Table 2).

Habitat degradation in the flyway

In the predicted suitable wetland sites (Fig. 1), for all eight species, 4% of the landscape was covered by water, and 26% and 21% of the landscape by grassland and cropland, respectively. The water area in suitable wetland sites in both non-breeding and breeding ranges of all eight species decreased during the 1992–2012 period, mainly in Southeast China, South Korea, Japan, Mongolia, and Northeast Russia (Fig. 2a).

As illustrated by the negative change in corresponding landscape variables in each grid, 43, 51, and 45% of the landscape experienced wetland loss, fragmentation, and isolation, respectively (Fig. 2).

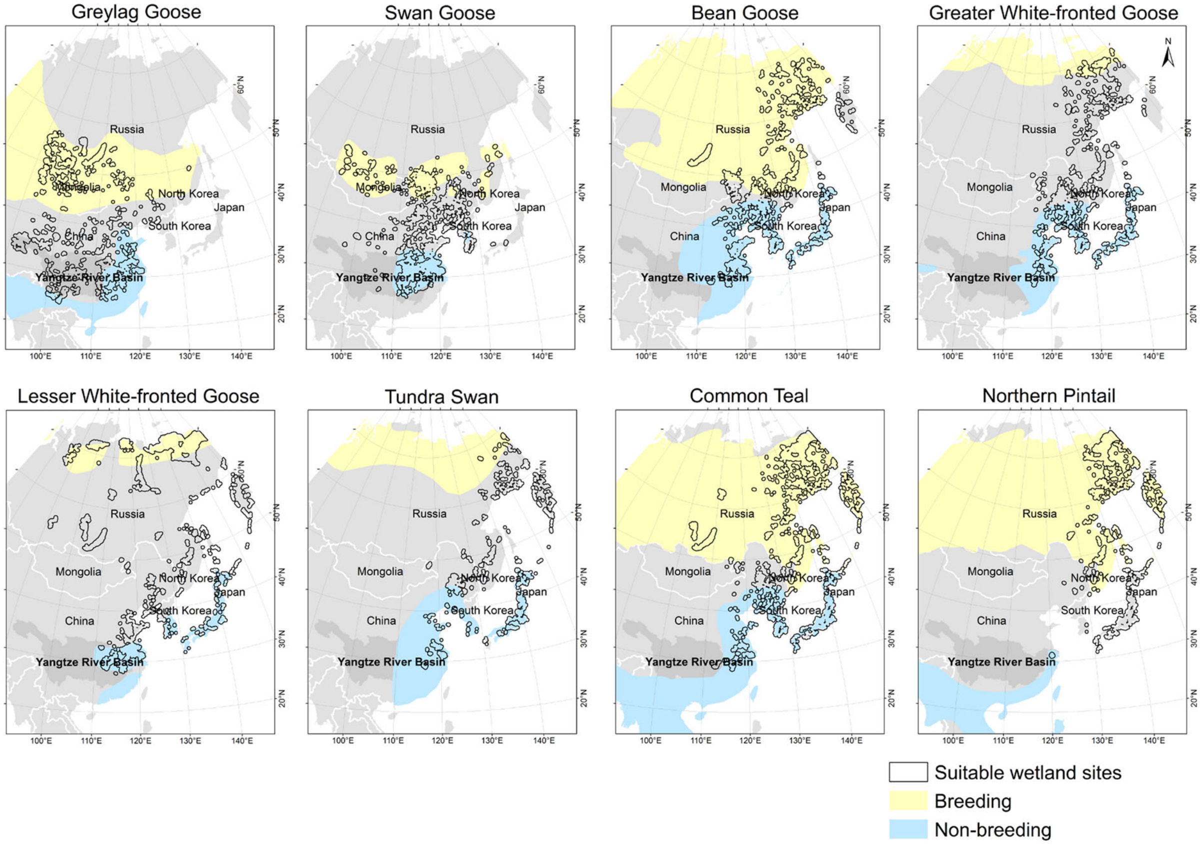


Fig. 1 Suitable wetland sites (hollow polygon with black border) for eight waterfowl species in the East Asian-Australasian Flyway. The ranges of suitable wetland sites were used for subsequent analysis, and included suitable lakes and a 32.5-km buffer around each of the suitable lakes

The three processes of wetland degradation happened simultaneously in 27% of the landscape, specifically in their non-breeding grounds in the Middle and Lower Yangtze River, Lower Yellow River, and Japan (Fig. 2). Habitat availability improved in inland regions, including the Upper Yellow River, Korea, Mongolia, and Russia, which are important breeding grounds for the study species, as indicated by an increase in wetland area and a decrease in the level of wetland isolation (Appendix S7).

Species-dependent effect of habitat degradation

The eight species were all exposed to wetland loss, fragmentation, and isolation in their non-breeding grounds in China and Japan, but their breeding grounds improved in both Mongolia and Russia. Although the configuration of wetlands improved in the stopover areas of the bean goose, greater white-fronted goose, and tundra swan, who pass both China and Russia during migration, the other species were affected by wetland loss, fragmentation, and isolation in their stopover areas, especially for those species with stopover areas in China and Japan (Appendices S3 and S4). Generally, the migratory species were affected by habitat degradation in the southern part of their seasonal distributions, and their habitat availability improved in the northern part (Fig. 3).

During 1992–2012, the wetland availability increased (or decreased less rapidly) with increasing latitude (GLM, $\beta = 0.004$, $t = 17.66$, $DF = 4619$, $P < 0.01$), and species with shorter and broader migration corridors had a significantly larger increase in wetland availability than species with longer and narrower migration corridors ($\beta = 0.016$, $t = 2.50$, $P = 0.01$). Similarly, the wetlands were less fragmented and isolated at higher latitude (GLM for wetland fragmentation, $\beta = 0.007$, $t = 17.64$, $DF =$

Table 2 Results of the logistic regressions of environmental factors on species presence for eight waterfowl species, showing the performance of the best models and regression coefficients (coefficient) for environmental factors included the best models

Model	Coefficient	SE	z-value	p value
Greylag goose (N = 178, AIC = 162.2, ΔAIC = 1.7, accuracy = 76.4%)				
(Intercept)	− 3.385	1.325	− 2.556	0.011*
Lake area [log(km^2)]	1.137	0.252	4.516	< 0.001***
Grass and crop resources [log(km^2)]	0.520	0.407	1.276	0.202
x	− 0.001	0.0002	− 5.088	< 0.001***
Swan goose (N = 114, AIC = 438.4, ΔAIC = 2.2, accuracy = 72.8%)				
(Intercept)	− 1.216	0.656	− 1.854	0.064
Lake area [log(km^2)]	0.822	0.146	5.628	< 0.001***
Grass and crop resources [log(km^2)]	0.399	0.198	2.022	0.043*
X	− 3.628e−04	1.348e−04	− 2.692	0.007**
x^2	− 6.455e−07	1.159e−07	− 5.570	< 0.001***
Bean goose (N = 394, AIC = 400.7, ΔAIC = 1.0, accuracy = 68.5%)				
(Intercept)	− 3.841	1.108	− 3.467	< 0.001***
Lake area [log(km^2)]	0.374	0.369	2.222	0.026*
Grass and crop resources [log(km^2)]	1.280	0.351	3.650	< 0.001***
x	1.472e−03	2.638e−04	5.579	< 0.001***
x^2	− 7.548e−07	1.715e−07	− 4.401	< 0.001***
Greater white-fronted goose (N = 714, AIC = 733.0, ΔAIC = 1.2, accuracy = 78.4%)				
(Intercept)	− 3.528	1.143	− 3.088	0.002**
Lake area [log(km^2)]	0.476	0.137	3.485	< 0.001***
Elevation [log(m)]	− 0.302	0.172	− 1.756	0.079
Grass and crop resources [log(km^2)]	1.383	0.333	4.153	< 0.001***
x	2.672e−03	3.004e−04	8.895	< 0.001***
x^2	− 1.513e−06	1.814e−07	− 8.342	< 0.001***
Lesser white-fronted goose (N = 114, AIC = 126.2, ΔAIC = 1.5, accuracy = 72.8%)				
(Intercept)	3.116	0.978	3.187	0.001**
Lake area [log(km^2)]	0.780	0.294	2.655	0.008**
Elevation [log(m)]	− 1.821	0.460	− 3.959	< 0.001***
x	4.268e−04	2.434e−04	1.753	0.080
Tundra swan (N = 446, AIC = 440.1, ΔAIC = 0.5, accuracy = 78.3%)				
(Intercept)	− 6.468	1.473	− 4.391	< 0.001***
Elevation [log(m)]	− 0.660	0.185	− 3.573	< 0.001***
Grass and crop resources [log(km^2)]	2.231	0.417	5.350	< 0.001***
x	1.741e−03	1.934e−04	9.008	< 0.001***
Common teal (N = 816, AIC = 893.0, ΔAIC = 1.0, accuracy = 75.5%)				
(Intercept)	− 1.979	0.614	− 3.222	0.001**
Lake area [log(km^2)]	0.562	0.103	5.446	< 0.001***
Grass and crop resources [log(km^2)]	0.470	0.194	2.425	0.015*
x	1.187e−03	1.075e−04	11.046	< 0.001***
x^2	− 1.315e−07	7.755e−08	− 1.695	0.090
Northern pintail (N = 2186, AIC = 1873.4, ΔAIC = 0.9, accuracy = 81.0%)				
(Intercept)	− 2.704	0.558	− 4.846	< 0.001***
Lake area [log(km^2)]	0.298	0.079	3.748	< 0.001***
Elevation [log(m)]	− 0.253	0.096	− 2.640	0.008**

Table 2 continued

Model	Coefficient	SE	z-value	p value
Grass and crop resources [log(km^2)]	0.647	0.154	4.211	< 0.001***
x	1.669e−03	1.044e−04	15.997	< 0.001***
x^2	1.252e−07	7.163e−08	1.748	0.080

ΔAIC is the difference between the AIC values of the best model and the second-best model (Appendix S2). Grass and crop resources were measured by the area of grasslands and croplands within the 32.5-km buffer surrounding each lake; x = centre x coordinate of each lake under the azimuthal equidistant projection. "***", "**", "*", "'" means the estimated regression coefficient was significant at 0.001 level, 0.01 level, 0.05, and 0.1 level, respectively

4619, $P < 0.01$; GLM for wetland isolation, $\beta = 0.009$, $t = 12.85$, $DF = 4619$, $P < 0.01$), and species with shorter and broader migration corridors had significantly less habitat fragmentation and isolation than species with longer and narrower migration corridors ($\beta = 0.088$, $t = 8.31$, $P < 0.01$; $\beta = 0.049$, $t = 2.77$, $P = 0.01$). Although wetland area for species with longer and narrower migration corridors increased at higher latitudes, that for species with shorter and broader migration corridors and a more western distribution increased more between 30 N–50 N in the areas of the Upper Yellow River and Mongolia (Fig. 3).

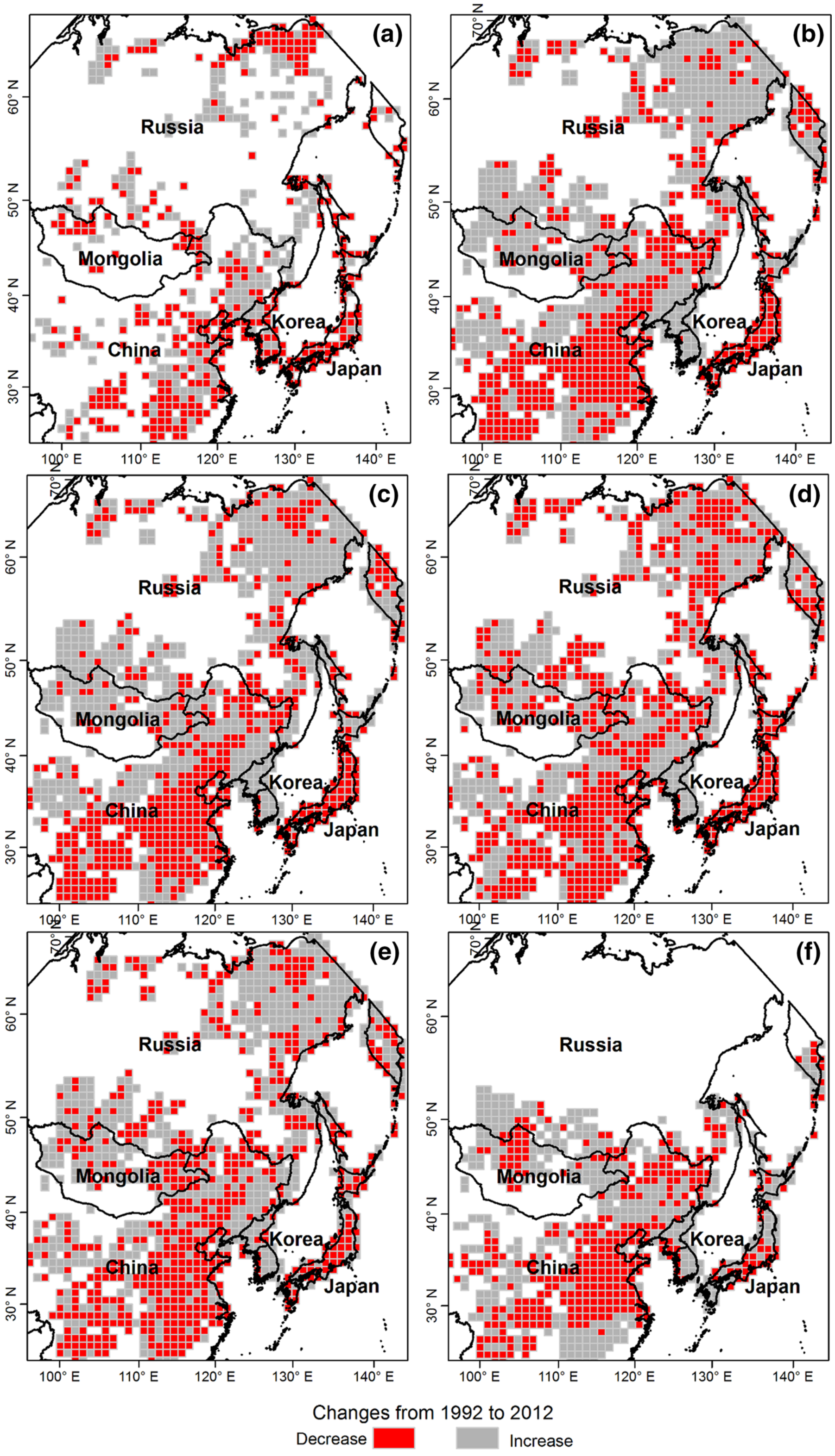
Discussion

The seasonal distributions of migratory waterfowl species determine the extent to which they are exposed to habitat degradation, which varies from place to place. As for migratory waterfowl in the East Asian–Australasian Flyway, habitat availability simultaneously degraded in the southeastern part of the flyway, i.e., in the coastal regions in China and Japan, but improved in inland regions of the western part of flyway (Fig. 2). Species with longer and narrower migration corridors that concentrate their migrations along the eastern coast could benefit less from improved habitat conditions in the southern part of their migration flyway compared to those with shorter and broader migration corridors. However, species with longer and narrower migration corridors could reach improved habitat conditions in Russia, in the northern part of their distribution range.

Areas of grassland and wetland in the suitable wetland sites in southern and eastern China and Japan decreased from 1992 to 2012 (Fig. 2b and c), and those areas could become spatial bottlenecks for species with main stopovers in these regions. Migratory species with spatial bottlenecks in degraded regions could be less resilient to habitat changes because of limited alternatives (Berger et al. 2008; Sawyer et al. 2009). These species must either skip the degraded wetlands or accept suboptimal conditions (Weber et al. 1999), leading to increased costs of migration, and consequently increased mortality during migration, and probably reduced efficiency of energy intake and reproduction. It could be difficult for the species experiencing successive habitat loss while migrating from their non-breeding to breeding grounds to replenish energy stores and maintain optimal body reserves for reproduction.

By investigating patterns of habitat change at the flyway scale, we further highlight the relationship between migratory extent and species-specific effects of environmental changes. Previous studies have found that migratory extent can affect species resilience to environmental changes. Species with a longer migration distance (Sanderson et al. 2006; Morrison et al. 2013), a smaller non-breeding area compared to breeding area (Gilroy et al. 2016), and a larger reliance on specific regions (e.g., South America and Yellow Sea tidal mudflat) are more vulnerable compared to others (North American Bird Conservation Initiative 2012; Studds et al. 2017). These facts can be explained when we relate their distributions to spatial patterns of habitat degradation at a flyway scale. Species occupying broader extent with more parallel alternative sites have plasticity in their reaction to habitat degradation. Species with shorter and broader migration corridors migrate across both degraded landscapes in the east and areas that have increased habitat availability in the west of the flyway. Despite the shorter migration distance of these species compared to the other study species, their migratory dispersion (i.e., larger non-breeding range size relative

Fig. 2 Spatial patterns in changes in landscape metrics from 1992 to 2012. **a** Water loss as measured by the change in total water area; **b** grassland loss as measured by the change in total grassland area. **c** Wetland availability as measured by the change in the total wetland area; **d** wetland fragmentation as measured by the change in the mean patch area of wetlands; **e** Wetland isolation as indexed by the change in the Proximity Index of wetland patches; **f** changes in agriculture resources as measured by the change in the total cropland area. A negative value indicates a decrease in corresponding landscape metrics



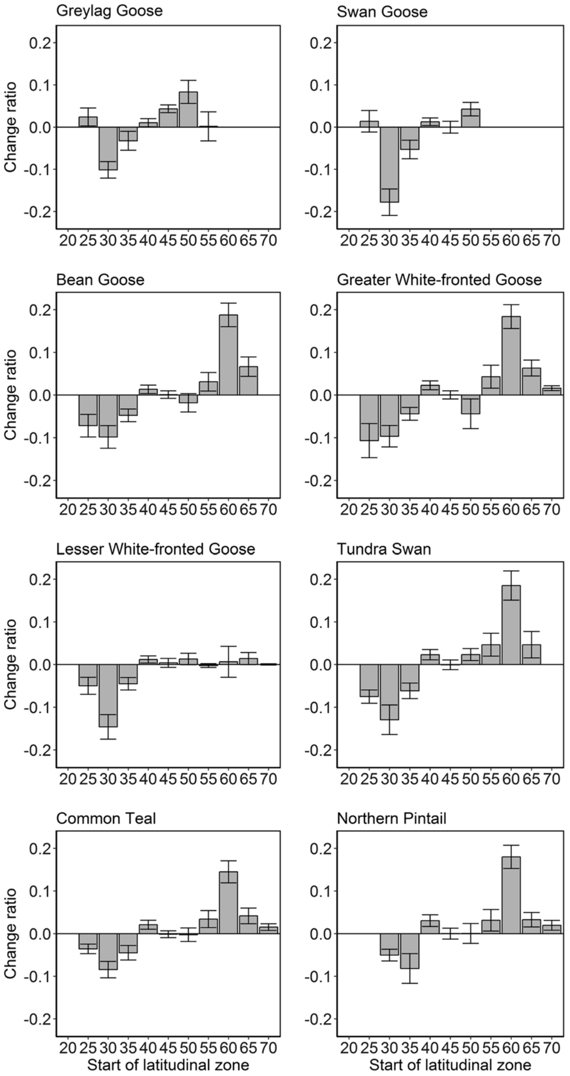


Fig. 3 Latitudinal patterns of change ratio (mean ± SD) of wetland availability (water surface and surrounding grasslands) in the suitable wetland sites from 1992 to 2012; x-axis represents five-degree latitudinal zones. A negative value indicates a decrease in area of wetlands in the corresponding latitudinal zone while a positive valued indicates an increase

to breeding) influences their resilience to habitat degradation. GPS tracking data also have shown that the swan geese from Mongolia migrate over a broad front, using a parallel configuration of stopover sites, although these geese share the same non-breeding and breeding grounds (Batbayar 2013). Swan geese can use stopover sites located at the western part of their flyway, where habitat degradation of stopover sites is lower than in the eastern part.

The wetlands of the East Asian–Australasian Flyway have been threatened by habitat loss, fragmentation, and isolation over the past two decades, which can subsequently impact migratory waterfowl by depleting resources and isolating wetland sites. Wetland degradation in eastern China and Japan contributed most to habitat destruction in the flyway from 1992 to 2012, partly as a consequence of rapid urbanization and socioeconomic development in East Asian countries since 1992 (Seto and Fragkias 2005). Wetlands on their non-breeding grounds with intensive human activities lost much of their area, triggering a human–wildlife conflict in which birds and people compete for resources (Fox et al. 2016; Jia et al. 2018). China has made rapid economic development since the economic reform in 1978, which is accompanied by accelerating environmental degradation, e.g., decreasing wetland area (Liu and Diamond 2005). Agricultural expansion is one of the most important threats to wetlands by forms of wetland conversion or water drainage for irrigation (Liu and Diamond 2005; Niu et al. 2012), and pollution and insufficient funding for protection are other contributing factors to wetland degradation (Liu and Diamond 2005). The coastal regions are confronted with larger problems compared to inland areas because of increased human pressure and sea-level rise, e.g., a considerable part of Japanese wetlands is threatened (Nicholls 2004; de Boer et al. 2011; Iwamura et al. 2013). On the contrary, natural habitats have recovered in the temperate zones of Russia due to a low human density and a widespread land abandonment since the sweeping reorganization of the Russian agriculture in 1990s (Grishchenko and Prins 2016).

Natural grasslands, as the primary foraging areas for waterfowl, are vulnerable because they are more sensitive to climate change than most human land-use types (Li et al. 2017c). Agriculture expanded around most wetlands and increased food resources for waterfowl, according to our modelling. For example, some wetlands in southeastern China are efficiently cultivated with multiple rice farming systems (Li et al. 2017a). However, these benefits might be a trade-off against greater human disturbance around these wetlands and increased wetland loss to land reclamation. Farmlands reclaimed in or around lakes and wetlands, sacrifice roosting and primary foraging sites (e.g., recessional grasslands) of waterfowl. Thus, waterfowl species are also more confined to their natural habitats instead of exploiting surrounding farmlands in their non-breeding grounds, and they tend to select habitats with lower human pressures in China (Yu et al. 2017; Li et al. 2017b). Moreover, there are other forms of habitat degradation for migratory waterfowl which have not been measured by the metrics quantified in our study, but can decrease waterfowl species diversity and reduce wetland quality, e.g., pollution with pesticides and heavy metals, changes in water levels by dams, poaching and hunting activities, and low efficiency of local conservation regulations (MaMing et al. 2012; Aharon-Rotman et al. 2017). In the future, ecological restoration projects considering these factors might offer some potential (An et al. 2007; Li et al. 2015) to conserve critical wetlands in the Middle and Lower Yangtze River, Lower Yellow River, and Japan.

Wetland degradation poses severe challenges to migratory species because wetland loss can reduce local abundance and species richness (Mora et al. 2011). Considering each wetland patch as an island surrounded by suboptimal or unsuitable habitats, both the loss of wetland area and isolation from other wetlands can trigger local extinction of populations (MacArthur and Wilson 1967; Purvis et al. 2000). The vulnerability of a population increases when even only a part of the migration network across a large spatial extent is affected (Iwamura et al. 2013). The population decline of migratory birds in relation to habitat degradation in the East Asian–Australasian Flyway has therefore triggered concern (Syroechkovskiy 2006; Cao et al. 2010; Sutherland et al. 2012), as East Asian populations of bean goose, greater white-fronted goose, lesser white-fronted goose, common teal, swan goose, and northern pintail are generally decreasing (Syroechkovskiy 2006; Cao et al. 2010; Wetland International 2017). Previous studies have suggested that a couple of bottleneck sites in their migration network explain these population declines. For example, the Yellow Sea tidal mudflat has shrunk by more than 65%, and consequently, the migratory shorebirds that highly rely on the Yellow Sea tidal mudflat experienced large population declines (Studds et al. 2017). The effect of habitat degradation on population size, especially for those species that use multiple stopover sites, depends not only on the overall extent of habitat degradation (Rogers et al. 2010; Iwamura et al. 2013), but also on where this degradation occurs (Runge et al. 2014). Our results demonstrate that habitat degradation in the migration flyway has a strong spatial component, which may explain differences in the population dynamics of migratory waterfowl species.

Because migratory species might be able to respond to habitat degradation by altering migration routes, future studies should focus on both specific regions and on the integrity of the whole migration network and on the plasticity of the species in terms of migratory movements and visited stopover sites. Hence, a network approach is required to better understand changes in migration strategy and population dynamics of migratory species. Remote-sensing techniques and temporal land cover data allow us to monitor the environmental changes at flyway scale (Si et al. 2015). There is, therefore, a demand for higher-accuracy and finer-resolution land cover datasets to support studies on the large-scale environmental changes in the framework of migration and conservation biology.

Conclusion

This study relates species seasonal distribution to species-dependent effects of habitat degradation in the migratory flyway. We have demonstrated that eight waterfowl species in the East Asian–Australasian Flyway are all exposed to habitat degradation in their non-breeding areas, but that conditions around wetland sites improve with increasing latitudes. Comparing changes at the same latitude, wetland sites for species with longer and narrower migration corridors degraded more from 1992 to 2012 than for species with shorter and broader migration. We conclude that migratory species with narrower distributions and longer migration distances are exposed to a higher level of habitat degradation because they have fewer parallel sites to provide alternative stopover, roosting, or foraging sites when habitat is degraded or lost. Hence, selection of important conservation regions for migratory birds should not only depend on local conditions of wetland sites but also take species-specific seasonal distributions into account. Especially, more efforts should be targeted along the migration routes of species with a narrow seasonal distribution and spatial bottlenecks in degraded regions of the flyway. Moreover, it is necessary to limit reclamation of wetland resources and unrestrained water drainage in regions of the East Asian–Australasian Flyway because wetlands in the Middle and Lower Yangtze River, Lower Yellow River, and Japan are major non-breeding grounds as well as important stopover areas for many waterbird species.

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