



Impacts of habitat loss on migratory shorebird populations and communities at stopover sites in the Yellow Sea

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ABSTRACT

Migratory birds generally use one or more stopover sites for rest and/or refuelling during long-distance migration where a large abundance of diverse species can concentrate into temporary assemblages. Habitat loss at stopover sites has resulted in population declines for many species, in particular shorebirds along the East Asian-Australasian Flyway. However, the consequences of habitat loss on the characteristics of bird assemblages at specific stopover sites are still unclear. We compared the results of shorebird surveys during northward migration between an “early” study period (1996 to 2005) and a “late” study period (2013 to 2014) at 14 stopover sites on the Yellow Sea coast in China, where a large tidal habitat area for shorebirds was destroyed. The total tidal flat area decreased by 35.6%, while the total shorebird abundance decreased by 7.8%, suggesting increased competition for space and food among shorebirds at stopover sites. However, changes in bird abundance (−72.9% to +210.0%) were not significantly related to tidal flat area changes (−71.2% to −2.0%) at the sites. Bray–Curtis similarity analysis indicated that community composition significantly differed among sites, but was similar within sites between study periods. This suggests habitat conditions, which determine the composition of bird communities, exhibited consistent site differences between study periods. These results imply that habitat loss at one stopover site is unlikely to be offset by conserving others; thus, protecting an extensive number of existing key stopover sites is crucial for the conservation of migratory birds.

1. Introduction

Long-distance migratory birds depend on one or more stopover sites for resting and/or refuelling during migration (Faaborg et al., 2010; Newton, 2008). As a linkage between breeding and nonbreeding sites, stopover sites play a critical role in successful migration and population maintenance. The selection of resting and refuelling sites by migratory species, which is closely related to the long-term evolution of migration routes and stopover decisions, determines the regularity of occurrence and abundance of bird populations at stopover sites (Albanese and Davis, 2013). During migration, diverse species with large numbers of individuals form temporary communities at stopover sites. Bird

communities are determined by local environmental conditions (e.g., habitat and food conditions) and by the interactions among species (e.g., competition and predation) (Webb et al., 2010; Ydenberg et al., 2004). Understanding the spatiotemporal traits of bird populations and communities at stopover sites helps clarify the importance of the sites for migratory birds and facilitates the development of conservation plans.

Because of large variation in migration schedules among species, bird communities are dynamic at stopover sites with the arrival and departure of migratory birds (Zhou et al., 2016). Migratory birds (especially waterbirds) often exhibit high repeatability in migration timing and strong site fidelity in the use of stopover sites between years (Conklin et al., 2013; Mettke-Hofmann and Gwinner, 2003), which

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might be adjusted by endogenous programmes of migratory birds to match optimal conditions at specific times and sites along migration routes and at migration destinations (Åkesson and Helm, 2020; Conklin et al., 2013; Newton, 2008). This implies that the dynamic community at stopover sites exhibit consistent patterns between years. On the other hand, external factors, such as weather conditions, affect the migration and stopover decisions of birds. When the weather is unfavourable for migratory flights (e.g., headwind), birds might change their migration schedule and temporarily stay at some stopover sites, thus affecting the population sizes and community composition at the sites (Ma et al., 2011; Shamoun-Baranes et al., 2010).

Habitat loss usually impacts the use of stopover sites by migratory birds. Some species can adjust their migration behaviour when facing habitat loss/deterioration at stopover sites. For example, in the African-Eurasian flyway (EAAF), the migration route of Ruffs (*Philomachus pugnax*) has moved eastwards, apparently in response to habitat degradation at former stopover sites on the western migration route (Verkuil et al., 2012). In the Atlantic Flyway, greater snow geese (*Anser caerulescens*) changed their northward migration route in response to increased human disturbance in the hunting season (Béchet et al., 2003). Similarly, human disturbance resulted in a redistribution of Svalbard pink-footed geese (*Anser brachyrhynchus*) among their stopover sites along the migration route in Europe (Klaassen et al., 2006). In the East Asian-Australasian Flyway, recent tracking of the migration of great knots (*Calidris tenuirostris*) revealed that during northward migration, some individuals remained on the coasts in south China, where fewer records were reported previously (Chan et al., 2019), and tracking of the migration of bar-tailed godwits (*Limosa lapponica*) demonstrated that birds prolonged their stopover in the Yellow Sea region in recent years (Conklin et al., 2021). Both of these examples are likely to be the result of habitat loss and degradation in the Yellow Sea region. These spatiotemporal changes influence both bird abundance and community composition at stopover sites. Clarifying the responses of birds to habitat changes at stopover sites is important for species conservation and habitat management. Although the effects of habitat loss at stopover sites on the population maintenance of migratory birds are well understood (e.g., Baker et al., 2004; Studds et al., 2017), information comparing community traits at stopover sites before and after environmental changes is generally lacking.

Many shorebirds are long-distance migrants. They generally concentrate in large flocks on tidal flats or roosting sites during migration periods (van de Kam et al., 2004). In the East Asian-Australasian Flyway, the Yellow Sea (including the Bohai Sea) coasts are the most important stopover region, providing refuelling stations for millions of shorebirds during migration between breeding sites in Siberia and Alaska and nonbreeding sites in Australasia and Southeast Asia (Bai et al., 2015; Barter, 2006; Hua et al., 2015). Field surveys have indicated that many shorebirds have suffered rapid population declines in recent decades (Clemens et al., 2016) and that such declines are closely related to the dramatic loss of tidal habitats at stopover sites along the Yellow Sea coast (Chen et al., 2019; Moores et al., 2016; Murray et al., 2014; Piersma et al., 2016; Studds et al., 2017). However, most evidence of population changes was collected from surveys in nonbreeding sites. Shorebird surveys over the past 20 years have identified important stopover sites for shorebirds in the Yellow Sea (Bai et al., 2015; Barter, 2002; Choi et al., 2020), while analyses of the relationships between environmental changes and spatiotemporal dynamics among shorebirds during migration are lacking. Whether shorebird populations at stopover sites have exhibited the same trends as those at nonbreeding sites and how the shorebird communities have changed at stopover sites are still unclear.

To advance our understanding of population and community changes among migratory shorebirds at stopover sites, we compared the results of shorebird surveys during northward migration between an “early” study period (1996 to 2005) and a “late” study period (2013 to 2014) at 14 stopover sites on the Yellow Sea coast in China. More

specifically, we determined changes in shorebird abundance and community composition between the study periods and tested three hypotheses: 1) populations exhibiting declining trends at nonbreeding sites also exhibited declining trends at stopover sites; 2) shorebird communities differed among stopover sites and between periods due to spatiotemporal differences in habitat condition; and 3) because habitat availability determines the use of stopover sites, we analysed areal changes in tidal habitats and tested that population and community changes among shorebirds are related to areal changes in tidal habitats at stopover sites.

2. Methods

2.1. Shorebird surveys

China's Yellow Sea region, which extends from the Yalu Estuary, Liaoning Province in the north, to the Yangtze Estuary, Shanghai in the south, has the largest intertidal flat in the world (Barter, 2002). The first comprehensive shorebird surveys along the Yellow Sea coast were conducted by teams led by Mark Barter between 1996 and 2005, hereafter termed the “early period” (Barter, 2002; Hua et al., 2015). The teams surveyed shorebirds during northward migration from late March at the southernmost site to mid-May at the northernmost site on the Yellow Sea coast (Fig. 1). The survey dates were selected to coincide as far as possible with the expected largest shorebird abundance during northward migration at each site. To facilitate bird surveys, sites were usually sub-divided and it took several days to complete a survey of each site. Each zone was usually surveyed on one day with good weather, and several days were therefore required to survey all of the zones at each site (Table S1). Most shorebirds forage on intertidal flats during low tide and rest at roosting sites during high tide. Consequently, survey schedules were arranged according to tidal rhythms: bird species and abundance were recorded by walking on intertidal flats during mid- and low tide, by counting birds when they congregate at pre-roosts on the upper intertidal flats as the tide approaches the sea wall, or by counting birds at roosting sites during high tide. Care was taken to avoid double counting. The abundance of unidentified species was also recorded during surveys. Because time was spent on training local people at each site during the shorebird surveys, only one to three sites were surveyed each year during the early period (Barter, 2002).

During northward migration in 2013 and 2014 (the late period), shorebirds along the Yellow Sea coast were surveyed again. A large area of intertidal flats that had existed in the early period had been lost through land claim and changed into other land use types, such as farmland and industrial zones, at many sites by the time that the late period surveys were undertaken (Chen et al., 2019). Because shorebirds concentrate in large flocks on the upper intertidal flats near the seawall and at roosting sites during high tide, we surveyed all the possible sections at each site. Thus, the later survey results well represent the total number of shorebirds on intertidal flats at the sites, making the data comparable between the early and late survey periods. In the early surveys, shorebirds were also recorded in some inland areas on the way to the survey sites. We excluded these records for further analysis because they were irregular and were not comparable between periods. To minimize the effects of migratory activities of birds on the data, we attempted to conduct late period surveys at each site on dates similar to those in the early period to minimize effects of migratory timing.

2.2. Areal changes in tidal flats

To quantify areal changes in tidal flats at the stopover sites between the early and late periods, we used Thematic Mapper (TM) and Enhanced Thematic Mapper (ETM+) images, specifically, the surface reflectance dataset (<http://ledaps.nascom.nasa.gov>), in the Google Earth Engine Cloud Platform. We extracted the lowest tidelines using the waterline mapping algorithm based on the time series of the land surface

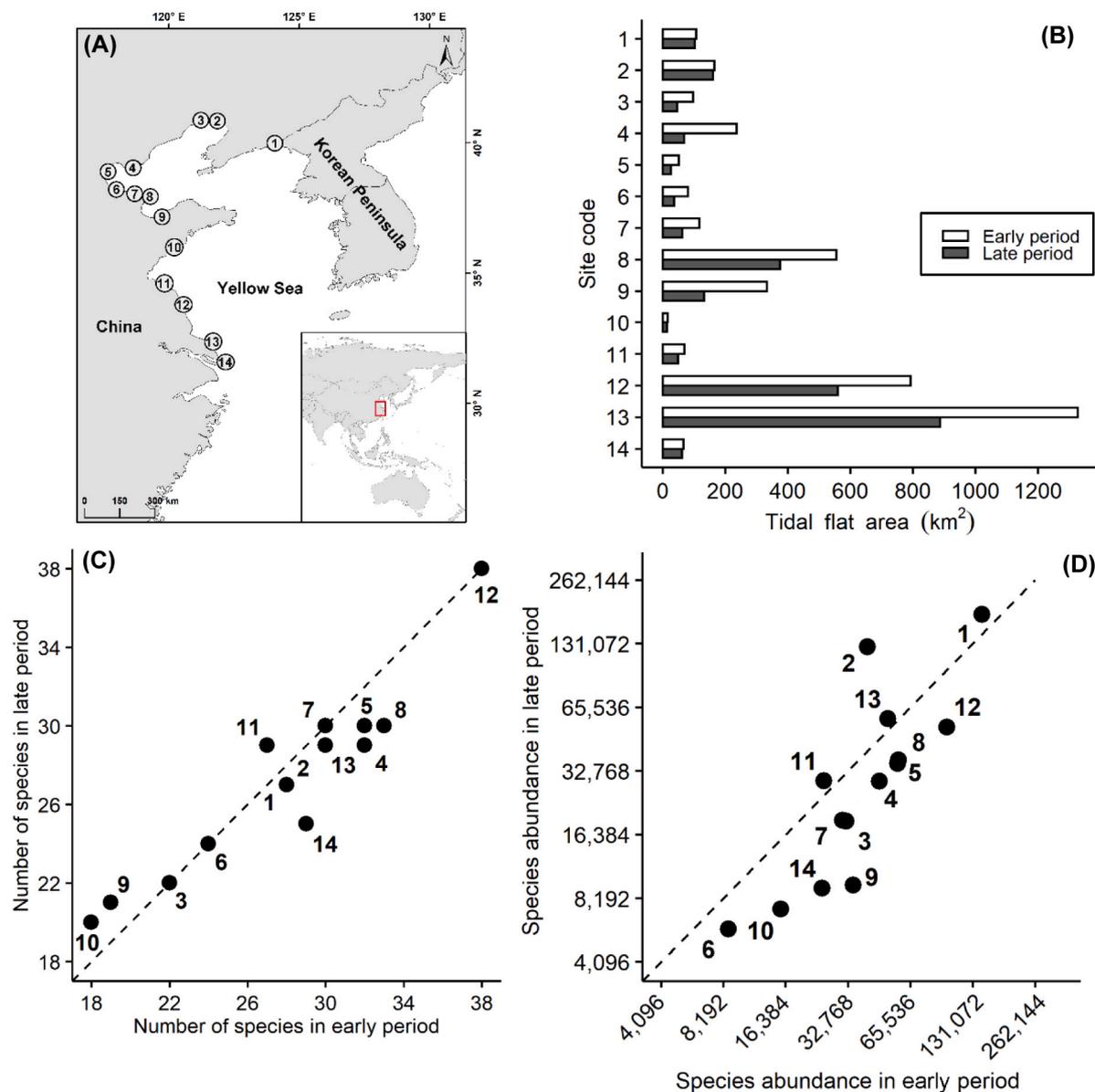


Fig. 1. Distribution (A), tidal flat areas (B), number of species (C) and species abundance (D) of the 14 stopover sites along China's Yellow Sea coast. Site codes: 1: Yalu Estuary, 2: Liaohe Estuary, 3: Jinzhou, 4: Northern Bohai Bay, 5: Tianjin, 6: Southwest Bohai Bay, 7: Southern Bohai Bay, 8: Yellow River Delta, 9: Laizhou Bay, 10: Jiaozhou Bay, 11: Lianyungang, 12: Yancheng, 13: Nantong, and 14: Chongming Dongtan.

water index and the normalized difference in the vegetation index (Chen et al., 2016). The waterline mapping algorithm was applied to all Landsat images to identify and map water bodies at each site. We generated water body frequency maps (with a range from 0 for no water body to 1 for 100% water body) at each site in the early period by stacking all of the low tide images from two years before the survey year to two years after the survey years (5 years totally) and in the late period by stacking all of the low tide images from 2012 to 2015. To reduce the effects of turbidity and other sources of observation error, we used 75% water body frequency as the threshold to delineate the lowest tidelines in each period (Chen et al., 2016). We selected one cloud-free Landsat image in the survey years to delineate artificial shorelines (seawalls and other artificial land-use types) at the sites through visual interpretation. The tidal flat area was calculated as the area between the artificial shorelines and the lowest tidelines, including both vegetated saltmarsh and bare tidal flat at each site (see details in Chen et al., 2016).

2.3. Data analysis

We used the survey data of 1 year at migration peak at each of the 14 sites in the early and late period respectively to detect changes in shorebird populations and communities between the periods. A total of 14 sites were surveyed with a difference of less than one week in the survey date between the early and late periods. For each site, if more than one survey was conducted within less than a one-week window in one period, we used the data recorded on the closest date to the early period for further analysis. We determined shorebird species and abundance at each site and at all 14 sites combined in each period. To provide comparability, only data recorded in the same zones in both periods were summarized. Because surveys at different sites were conducted on different dates, individual birds that stayed at multiple sites along the Yellow Sea during migration might be counted repeatedly, as indicated by satellite tracking data (e.g., Chan et al., 2019). However, because birds were surveyed using the same methods in the two periods, the results from the two periods are comparable.

Wilcoxon signed rank tests were used to compare the difference in species richness and abundance at the same sites between the two periods. Friedman tests were used to compare the differences in species richness and abundance among sites during the same period. We further compared abundance changes in species with abundance levels representing at least 1% of the total flyway population (Wetlands International, 2012) at one or more of the 14 sites.

Temporal and spatial differences in shorebird assemblages were explored using nonmetric multidimensional scaling (NMDS) ordination analysis with the Bray–Curtis dissimilarity distance matrix in the *vagan* package in R (Oksanen et al., 2021). The first three axes of the NMDS had a stress value of 0.13 ($R^2 = 0.98$ for nonmetric fit and 0.87 for linear fit), suggesting that the data were well represented in these three dimensions. Analysis of similarity (ANOSIM) based on Bray–Curtis distance matrices (Clarke et al., 2014) was then used to quantify the

differences in shorebird assemblages among sites in the same period and between periods at the same site. In ANOSIM, R values range from -1 to 1 ; a positive value suggests that bird assemblages within the same site between periods are more similar than bird assemblages between different sites within the same period, and a larger absolute value of R indicates a larger difference.

Because tidal flats are the major foraging habitats for shorebirds, we estimated the density of shorebird abundance on tidal flats (birds per hectare) according to bird counts on tidal flats or at high tide roosts at each site. We further compared the estimated density between the early and late periods using the paired *t*-test. Least squares linear regressions were used to relate the relationship between the areal changes in tidal flats and shorebird population changes and shorebird assemblage changes (community dissimilarity) among sites.

Table 1

Species and the total abundance of shorebirds recorded at 14 stopover sites along China's Yellow Sea coast and population trends at the flyway level based on published population trends in nonbreeding sites (Clemens et al., 2016; Moores et al., 2016; Studds et al., 2017; Wetlands International, 2012). Species that attained 1% of the total flyway population at one or more stopover sites in this study are shown in bold.

Species name	Scientific name	Total abundance		Proportional difference (%)	Population trend in nonbreeding sites
		Early period (1996–2005)	Late period (2013–2014)		
Oriental Pratincole	<i>Glareola maldivarum</i>	117	1	-99.15	–
Asian Dowitcher	<i>Limnodromus semipalmatus</i>	3,076	2,145	-30.27	Declining
Common Snipe	<i>Gallinago gallinago</i>	68	23	-66.18	–
Terek Sandpiper	<i>Xenus cinereus</i>	2,029	614	-69.74	Declining
Red-necked Phalarope	<i>Phalaropus lobatus</i>	0	220	–	Declining
Wood Sandpiper	<i>Tringa glareola</i>	2,360	477	-79.79	–
Marsh Sandpiper	<i>Tringa stagnatilis</i>	35,106	10,207	-70.93	–
Common Redshank	<i>Tringa totanus</i>	550	211	-61.64	–
Spotted Redshank	<i>Tringa erythropus</i>	7,535	2,330	-69.08	–
Common Greenshank	<i>Tringa nebularia</i>	2,539	2,003	-21.11	Declining
Grey-tailed Tattler	<i>Tringa brevipes</i>	6	1	-83.33	Declining
Spotted Greenshank	<i>Tringa guttifer</i>	4	58	1,350.00	Declining
Green Sandpiper	<i>Tringa ochropus</i>	7	2	-71.43	–
Common Sandpiper	<i>Actitis hypoleucos</i>	122	39	-68.03	–
Long-toed Stint	<i>Calidris subminuta</i>	114	12	-89.47	–
Temminck's Stint	<i>Calidris temminckii</i>	82	8	-90.24	–
Sanderling	<i>Calidris alba</i>	125	4,562	3,549.60	–
Sharp-tailed Sandpiper	<i>Calidris acuminata</i>	10,114	13,626	34.72	Declining
Red-necked Stint	<i>Calidris ruficollis</i>	34,848	14,649	-57.96	Declining
Dunlin	<i>Calidris alpina</i>	168,574	120,627	-28.44	Declining
Curlew Sandpiper	<i>Calidris ferruginea</i>	16,861	13,305	-21.09	Declining
Ruff	<i>Calidris pugnax</i>	26	5	-80.77	–
Broad-billed Sandpiper	<i>Calidris falcinellus</i>	1,048	1,304	24.43	–
Red Knot	<i>Calidris canutus</i>	27,131	16,837	-37.94	Declining
Great Knot	<i>Calidris tenuirostris</i>	124,208	194,988	56.99	Declining
Spoon-billed Sandpiper	<i>Calidris pygmaea</i>	1	11	1,000.00	Declining
Ruddy Turnstone	<i>Arenaria interpres</i>	316	645	104.11	Declining
Bar-tailed Godwit	<i>Limosa lapponica</i>	111,461	130,133	16.75	Declining
Black-tailed Godwit	<i>Limosa limosa</i>	12,413	4,592	-63.01	Declining
Eurasian Curlew	<i>Numenius arquata</i>	14,014	11,618	-17.10	–
Little Whimbrel	<i>Numenius minutus</i>	66	10	-84.85	–
Far Eastern Curlew	<i>Numenius madagascariensis</i>	8,076	2,021	-74.98	Declining
Whimbrel	<i>Numenius phaeopus</i>	7,095	1,392	-80.38	Declining
Grey Plover	<i>Pluvialis squatarola</i>	54,642	47,562	-12.96	Declining
Pacific Golden Plover	<i>Pluvialis fulva</i>	196	278	41.84	Declining
Long-billed Plover	<i>Charadrius placidus</i>	1	0	-100.00	Declining
Kentish Plover	<i>Charadrius alexandrinus</i>	16,244	12,117	-25.41	–
Lesser Sand Plover	<i>Charadrius mongolus</i>	3,994	2,888	-27.69	Declining
Greater Sand Plover	<i>Charadrius leschenaultii</i>	263	1,067	305.70	Declining
Grey-headed Lapwing	<i>Vanellus cinereus</i>	24	8	-66.67	Declining
Common Ringed Plover	<i>Charadrius hiaticula</i>	1	0	-100.00	Declining
Little Ringed Plover	<i>Charadrius dubius</i>	40	21	-47.50	–
Pied Avocet	<i>Recurvirostra avosetta</i>	902	3,087	242.24	–
Black-winged Stilt	<i>Himantopus himantopus</i>	2,235	556	-75.12	–
Eurasian Oystercatcher	<i>Haematopus ostralegus</i>	361	887	145.71	–

Note: –, the proportion of individual changes and population trends are unknown.

3. Results

3.1. Changes in species richness and abundance between periods

At the 14 stopover sites, a total of 668,995 individuals of 44 species were recorded in the early period, and a total of 617,146 individuals of 43 species were recorded in the late period (Table 1), which corresponded to 7.8% fewer birds counted from the early to the late period. Dunlin (*Calidris alpina*), great knot, and bar-tailed godwit were the most abundant species in both surveys, accounting for 60.4% and 72.2% of the total counts in the early and late periods, respectively (Table 1).

Species richness varied among sites (18 to 38 species) but was similar at the same site between the periods (Fig. 1C). In the early period, species richness was the greatest at Yancheng (38 species), followed by the Yellow River Delta (33 species) and Tianjin and Northern Bohai Bay (32 species each). In the late period, species richness was again largest at Yancheng (38 species), followed by Tianjin, southern Bohai Bay, and the Yellow River Delta (30 species each).

The total bird abundance varied among sites and between periods at the same site (Fig. 1D). In the early period, the highest abundance was recorded in the Yalu Estuary (145,518 birds), followed by Yancheng (98,728 birds) and the Yellow River Delta (57,549 birds). In the late period, the highest abundance was recorded again in Yalu Estuary (180,063 birds), followed by Liaohe Estuary (126,122 birds) and Nantong (57,606 birds). Compared with the early period, decreased abundance was recorded at ten sites (ranging from -72.9% to -32.5%), and increased abundance was recorded at four sites (ranging from +12.8% to +210.0%) in the late period. The increase in bird abundance in the Liaohe Estuary (by 210.0%) was mainly due to the presence of a large flock of great knots (estimated at 80,000 birds) during surveys in the late period (recorded by YC and DSM on May 15, 2014). If the flock of great knots was excluded from the dataset, the total bird abundance in the Liaohe Estuary increased by 13.4%.

No significant differences were found in species richness (Wilcoxon signed rank test, $Z = 1.22$, $r = 0.30$, $p = 0.2$) (Fig. 1C) or abundance (Wilcoxon signed rank test, $Z = 1.35$, $r = 0.36$, $p = 0.18$) (Fig. 1D) at the same site between the periods. There were, however, significant differences in species richness (Friedman test, $X^2 = 24.87$, $df = 13$, $p = 0.02$) (Fig. 1C) and abundance (Friedman test, $X^2 = 23.94$, $df = 13$, $p = 0.03$) (Fig. 1D) among sites in the same period.

A total of 25 species occurred in numbers equivalent to $\geq 1\%$ of the total flyway population at one or more of the 14 study sites (Table 2 & S2). Twelve of these 25 species were detected population changes (all exhibited population declines) in the early 2000s on the nonbreeding grounds (Table 1). Of these 12 species, 10 exhibited fewer records in total abundance (reduced by 13.0 to 80.4%), while higher numbers were

Table 2

Numbers of species representing $\geq 1\%$ of the total population in the flyway at each stopover site in the early period and in the late period. See details in Table S2.

Site name	Early period 1996–2005	Late period 2013–2014
Yalu Estuary	8	7
Liaohe Estuary	5	7
Jinzhou	5	7
Northern Bohai Bay	8	7
Tianjin	9	9
Southwest Bohai Bay	3	2
Southern Bohai Bay	4	6
Yellow River Delta	8	9
Laizhou Bay	4	3
Jiaozhou Bay	3	2
Lianyungang	7	6
Nantong	7	6
Yancheng	7	9
Chongming Dongtan	5	2

recorded in the later period for two species (increase by 16.8% for bar-tailed godwit and 57.0% for great knot) across all sites combined (Table 1 & S1).

3.2. Changes in shorebird communities

Although abundance of the same species changed substantially at many sites, the dominant species changed less at each site between the early and late periods (Table S3). For example, great knot and bar-tailed godwit were the dominant species in the Yalu Estuary; red knot (*Calidris canutus*) and curlew sandpiper (*Calidris ferruginea*) were the dominant species in North Bohai Bay in both periods. The NMDS ordination revealed that bird assemblages at a site were similar between the early and late periods (Figs. 2A & 2B). ANOSIM further indicated no significant differences in shorebird communities within the same site between the periods ($R = -0.01$, $p = 0.54$, Fig. 2C). However, dissimilarity of community structure was significantly higher between the sites than within the same site between periods ($R = 0.87$, $p = 0.001$, Fig. 2D).

3.3. Relationships between changes in tidal flat areas and shorebird populations

The total tidal flat area decreased by 35.6%, from 4017 km² in the early period to 2588 km² in the late period at all sites combined. Tidal flat loss was detected at all the 14 sites. More than half of the tidal flat was destroyed at Northern Bohai Bay, Laizhou Bay, Southwest Bohai Bay, and Jinzhou during the study period. Less tidal flat loss (<10%) occurred at Chongming Dongtan, Yalu Estuary, Jiaozhou Bay, and Liaohe Estuary (Fig. 1B).

The estimated density of shorebirds on a tidal flat varied largely among sites (from the lowest density of 38.5 birds/km² at Nantong to the highest density of 1350.0 birds/km² at Yalu Estuary in the early period; from the lowest density of 64.9 birds/km² at Nantong to the highest density of 1745.1 birds/km² at Yalu Estuary in the late period). During the study period, the estimated bird density increased at 7 sites (by 14.8–216.2%) and decreased at 5 sites (-60.2 to -5.0%). Although we did not detect a significant difference in estimated bird density at the sites between the periods (paired *t*-tests, $t = 0.41$, $df = 13$, $p = 0.69$), the density increased by 43.2% at all sites combined, from 166.5 birds/km² in the early period to 238.5 birds/km² in the late period.

No significant relationship was identified between changes in tidal flat areas and changes in shorebird abundance ($R^2 = 0.22$, $p = 0.09$) (Fig. 3A) and shorebird density ($R^2 < 0.001$, $p = 0.94$) (Fig. 3B) at the stopover sites. Additionally, no significant relationship was found between changes in tidal flat areas and dissimilarities among shorebird communities between periods ($R^2 = 0.001$, $p = 0.91$) (Fig. 3C). Results were consistent if the flock of 80,000 great knots was excluded from the data (Fig. S1).

4. Discussion

In the East Asian-Australasian Flyway, many shorebirds have suffered dramatic population declines over the past several decades (Hua et al., 2013; Piersma et al., 2016; Studds et al., 2017), mainly due to habitat loss and degradation at stopover sites in the Yellow Sea (Piersma et al., 2016; Studds et al., 2017). Our study indicated that at 14 stopover sites in the Yellow Sea, the total bird counts exhibited a decline, while changes in bird abundance levels varied among species and sites during the study period. We found that the community composition of shorebirds largely varied among sites but generally remained stable during the study period at the same site, even though a large area of tidal habitats was lost. Although the combined habitat area decreased by 35.6%, the number of birds using the areas only decreased by 7.8%. We did not find significant correlation between either population changes nor community changes in shorebirds and areal changes in tidal habitat at stopover sites in this study. Because the number of birds decreased

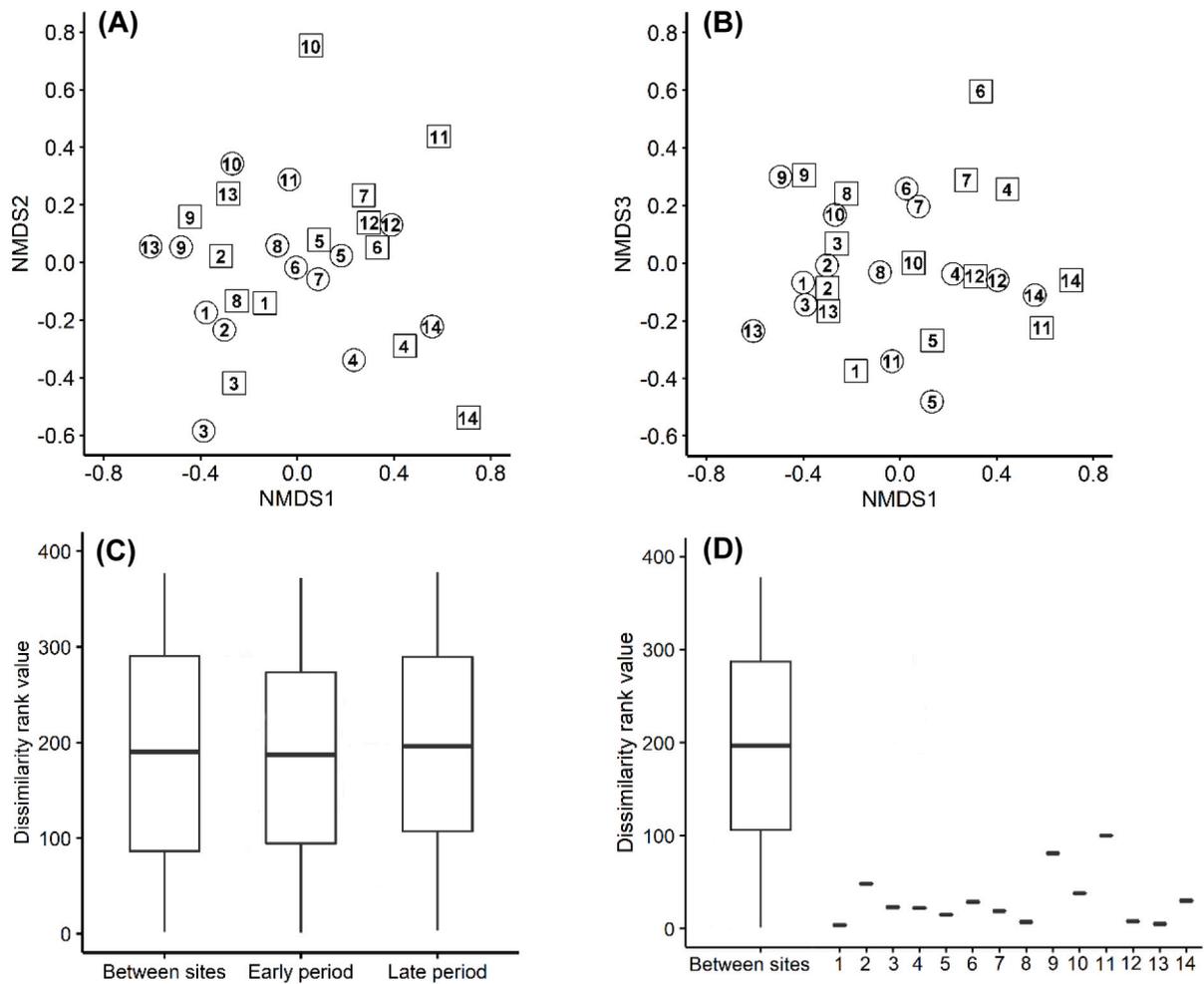


Fig. 2. The first three axes of NMDS ordination of shorebird communities (A: the first and second axes, B: the first and third axes), the dissimilarities among shorebird communities among sites between the early and late periods, in the early period, and in the late period (C) and the dissimilarities among shorebird communities between periods across all sites and between periods at each site (D) according to ANOSIM. In A and B, the squares represent the early periods, and the circles represent the late period. In A, B, and D, the numbers in the figures are site codes, which are defined in Fig. 1. We jittered some overlapped points for clearer depiction.

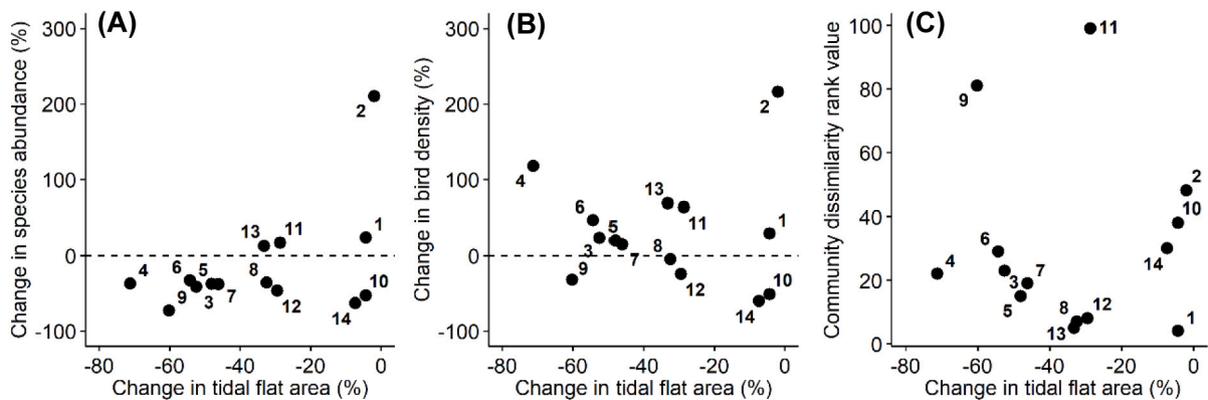


Fig. 3. The relationship between the change in the tidal flat area and the change in the abundances of shorebird (A), between the change in the tidal flat area and the change in the density of shorebird (B) and between the change in the tidal flat area and changes in dissimilarities among the community structure of shorebirds (C) at the stopover sites. Site codes refer to Fig. 1.

much less than the area, the combined estimated bird density on tidal flats has increased dramatically, by 43.2% overall, suggesting increased competition for resources at stopover sites.

4.1. Shorebird abundance at stopover sites

Although bird surveys covered the same zones and were conducted on similar dates between the early and late periods at the same stopover

sites, changes in shorebird counts during the study periods did not always exhibit the same population trends as those at nonbreeding sites, which is inconsistent with our first hypothesis. Similar results have been reported based on analysis of the data from shorebird surveys in South Korea (Moore et al., 2016) and waterbird surveys along China's coasts (Choi et al., 2020), which might be due to the non-mutually exclusive reasons below.

First, the distribution of a species throughout its range is often uneven due to differences in habitat availability and quality. Generally, birds prefer to concentrate in high-quality habitats; thus, bird abundance levels are often close to the carrying capacity at sites. When the total bird abundance changes, bird abundance may decrease substantially in low-quality habitats but remain stable in high-quality habitats (Gill et al., 2001). In this study, all of the surveyed sites have been identified to be critical habitats for shorebirds (Barter, 2002) and include all of the national nature reserves that have been designated for conserving shorebirds along the Yellow Sea in China (Ma et al., 2019). As a result, changes in the abundance of the total populations may be difficult to detect because surveys focused on high-quality habitats in this study. Moreover, habitat loss outside the surveyed sites could displace shorebirds towards the survey sites. For example, red knot exhibited an obvious population decline in the flyway, while its abundance at Nanpu, the most important stopover site for the red knot in the EAAF, largely increased during the 2000s, which is likely due to habitat loss in the surrounding regions forcing more birds into the remaining habitat (Yang et al., 2011). Similarly, habitat loss at the survey sites could also displace shorebirds towards other sites.

Second, migratory birds can fine-tune their migration timing and stopover decisions according to weather and body conditions (Hua et al., 2017; Ma et al., 2011; Shamoun-Baranes et al., 2010), which causes migration schedules to vary among years at the same sites. At Chongming Dongtan in the south Yellow Sea, for example, bird abundances are much higher during periods with headwinds than during those tailwinds because headwinds are less suitable for migratory flight, causing more birds to stay and fewer to depart (Ma et al., 2011). Because the use of stopover sites along the flyway is interdependent (Klaassen et al., 2006), both the current and the previous weather conditions that the birds experience affect migration timing and can thereby cause interannual differences in numbers at the same time of year and at the same stopover site.

Third, bird populations exhibit rapid turnover at some sites, especially at temporary stopover sites. For example, great knot individuals stay for an average of 2.3 days (the median is 1 day) at Chongming Dongtan during northward migration (Ma et al., 2013), suggesting that bird abundance levels can substantially change even between successive days at the same stopover site, masking population changes between periods in the flyway. In the late period of the current study, although we reported the largest flock of great knots (80,000 birds) recorded in recent decades, the flock was not recorded in earlier or subsequent surveys at the site (Choi et al., 2020). However, a similar number of great knots was recorded at a stopover site nearby (approximately 60,000 birds at Gaizhou), which was not covered in the surveys in the early period (Melville et al., 2016), which suggests that some individuals might move to other stopover sites when habitat quality declines at a site (Ke et al., 2019; Melville et al., 2016). Recent studies have also shown that the shortage of high-quality food in the Yalu Estuary caused an early departure of late-arriving great knots, resulting in a decrease in abundance during the migration peak at the site (Ke et al., 2019), which suggests that changes in habitat-associated migration behaviour may greatly affect bird abundance levels at stopover sites.

Although quantifying population dynamics at the flyway level based on bird surveys at stopover sites is difficult, such surveys provide information for evaluating the importance of stopover sites. For example, the Ramsar Convention has adopted the "1% criterion" by which a site is considered to be of international importance if it regularly supports 1% of a population of a waterbird (Ramsar Convention Secretariat, 2010).

The "1% criterion" has been used to identify such sites in the Yellow Sea (Bai et al., 2015; Barter, 2002). Bird surveys can be used to detect the consequences of habitat changes at the local scale. The destruction of the Saemangeum area in South Korea through reclamation, formerly the most important stopover site for shorebirds in the Yellow Sea, resulted in dramatic declines in a number of shorebird species, demonstrating the adverse effects of loss of tidal wetlands (Moore et al., 2016). Survey data from stopover sites can also be used to guide conservation actions. In 2019, *Migratory bird sanctuaries along the coast of the Yellow Sea-Bohai Gulf of China (Phase I)* were added to the World Heritage List (World Heritage Committee, 2019). This nomination was strongly supported by the results of surveys at stopover sites along the Yellow Sea over the past two decades.

Some species are scattered over a large region during breeding and nonbreeding periods, but have a highly clumped distribution at some stopover sites, probably due to their special habitat requirements during migration (e.g., Asian dowitcher (*Limnodromus semipalmatus*), spotted greenshank (*Tringa guttifer*), and spoon-billed sandpiper (*Calidris pygmaea*) in the Yellow Sea, Peng et al., 2017; Yang et al., 2021). In this case, bird surveys at stopover sites can be critical to population estimation. For example, the population of endangered spotted greenshank was estimated at 400–600 birds (Wetlands International, 2012), while counts at a stopover site in Jiangsu gave a total of 946 birds (Choi et al., 2020; Peng et al., 2017), indicating that the population was previously underestimated. Detailed analysis of re-sightings of marked birds at a stopover site has also allowed a global population estimate for the critically endangered spoon-billed sandpiper (Green et al., 2021).

Some shorebirds have advanced breeding timing, and thus migration timing as well probably, along with climate warming in the breeding sites in the Arctic (Høye et al., 2007). However, phenology advancements of shorebirds vary among breeding sites and species (Kwon et al., 2018; Reneerkens et al., 2016), suggesting complex impacts of climate changes. In this study, both surveys at the same sites were conducted on the similar date, thus possible changes in migration timing might have affected the survey results. However, migration periods of shorebirds generally last more than half a month at stopover sites (e.g., Choi et al., 2009; Zhou et al., 2016); our surveys at each site were conducted at migration peak when bird abundance was the largest. These suggest that the impact of advancement of migration timing on the results, if it occurred, would be limited.

4.2. Shorebird communities at stopover sites

We found that shorebird populations and communities largely differed between sites in the Yellow Sea, which is consistent with our second hypothesis, and is closely related to the special habitat and food conditions that shape the different shorebird populations and communities among stopover sites. In general, shorebirds forage on macrobenthos on tidal flats at stopover and nonbreeding sites, but differ in the preferences for microhabitat and food among species (Jing et al., 2007). As a result, habitat and food conditions determine the distribution of shorebirds among stopover sites. For example, both great knots and red knots, mainly forage on bivalves on tidal flats. During northward migration, great knots, which are larger than red knots, tend to aggregate in the Yalu Estuary (Choi et al., 2015), while red knots tend to aggregate in Nanpu (Rogers et al., 2010). This might be related to the difference in food availability between the two sites: *Potamocorbula laevis*, the major food of both species at the two sites, was generally larger in size at Yalu Estuary and more suitable for great knots (Choi et al., 2017; Zhang et al., 2019), while smaller sized *P. laevis* is dominant at Nanpu and is more suitable for red knots (Yang et al., 2013). Because migratory birds experience strong pressure to arrive at the migration destination on time, suitable and superabundant food is critical for their rapid fuel deposition at stopover sites (Battley et al., 2005).

Recent studies have suggested that shorebirds can use alternative sites or change migration timing when facing habitat loss or degradation

at stopover sites in the Yellow Sea (Conklin et al., 2021). This may influence both bird abundance and communities at the sites. However, inconsistent with our second hypothesis, although bird abundances largely changed, bird communities were generally similar between periods at the same sites. Moreover, neither population changes nor community changes in shorebirds were related to areal changes in tidal habitat at stopover sites. This suggests that the use of stopover sites was not random by birds, which might be closely related to the different habitat conditions, including both abiotic conditions such as sediment and hydrology and biotic conditions such as food and interactions between species, among sites. Our results suggest that it might be difficult to find alternative sites of high quality when the original habitat is lost, especially in the Yellow Sea, where habitat loss by land claims has been a common phenomenon (Chen et al., 2019; Murray et al., 2014).

Dramatic habitat changes could lead to complete changes in the bird population and community at a site (Moore et al., 2016). In this study, not all the habitat was completely lost, and the remaining habitats may still retain the original traits at each site. This might lead to a relatively stable shorebird community between periods at the same sites. However, we found that the estimated bird density on tidal flats has increased by 43.2% after the substantial loss of tidal flats. This could aggravate the intra- and interspecific competition for limited space and food resources, as well as increase the risk of disease transmission (van Dijk et al., 2018). Migratory birds need to consume a large amount of food within a limited stopover period to accumulate sufficient fuel for the next phase of migratory flight. Increased competition and interference lead to a decline in foraging efficiency (Duijns and Piersma, 2014) and result in fitness costs that compromise the ability to migrate successfully (Baker et al., 2004).

In this study, the areal change in tidal flats was used as an indicator of changes in habitat condition. Although shrinkage of tidal flats results in habitat loss, habitat condition can also be affected by other factors. Over the past two decades, invasive smooth cordgrass (*Spartina alterniflora*) has spread rapidly along the Yellow Sea coast (Liu et al., 2018), forming dense monocultures that are unsuitable for shorebirds on tidal flats (Gan et al., 2009). As a consequence, habitat availability might be overestimated in regions with large areas of smooth cordgrass. In the Yalu Estuary, the area of tidal flats has decreased only slightly (4.27%), while the density of *P. laevis*, the major high-quality food for shorebirds, has significantly decreased (Zhang et al., 2018), which has resulted in a food shortage for great knots and other shorebirds that depend on *P. laevis*. However, we have limited knowledge of the food conditions for most stopover sites along the Yellow Sea coast (Peng et al., 2021; Zhang et al., 2018), on which further studies are required.

5. Conservation implications

Long-term survey bird data provide a basis to identify population trends and their drivers. We found that survey data collected at stopover sites should be used with great caution to infer population trends at the flyway level, however, they help to guide conservation policy and practice. Currently, there are multiple national shorebird surveys in some countries, such as China (Choi et al., 2020), South Korea (Moore et al., 2016), Japan (Amano et al., 2010), New Zealand (Riegen and Sagar, 2020) and Australia (Clemens et al., 2016), along the EAAF, with different protocols among countries. Regular surveys are still absent in some regions (e.g., in North Korea and Southeast Asia). In the future, comprehensive surveys using standardized protocols and with shared datasets along the entire flyway are critical for detecting changes in population and communities at key sites as well as for assessing responses to habitat changes at breeding, stopover, and nonbreeding sites.

Studies at the species level, especially those focused on habitat specialists, have found that some birds cannot successfully relocate to alternate sites if their major staging sites are lost (Fuller et al., 2021; Moore et al., 2016). According to our results at the community level, conserving habitats at other stopover sites cannot fully compensate for

the destruction of one stopover site. This study highlights that maintaining populations of migratory species depends on the conservation of an extensive number of existing key stopover sites along the flyway.

CRedit authorship contribution statement

ZJM designed and led the study; YC, DSM, and KT conducted field surveys in 2013 and 2014; XDW collected and analysed the data and wrote the manuscript with contributions from all of the coauthors.

Data and materials availability

The raw data from shorebird surveys can be acquired from the corresponding author.

Declaration of competing interest

The authors declare that they have no competing interests or relationships that could have appeared to influence the work reported in this work.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2022.109547>.

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