

Climate and land-use change reshape shorebird habitat networks in China's greater bay area: Trends from scenario-based projections

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ABSTRACT

Accelerated urbanization and land reclamation have caused widespread loss of coastal wetlands, reduced habitat availability and increased migration costs for shorebirds. However, the interactive effects of climate change and land-use transitions on habitat networks remain insufficiently understood, especially in rapidly developing bay regions. We developed a scenario-based framework to disentangle climate and land-use impacts on shorebird habitat networks. Integrating species distribution models, landscape connectivity assessments and circuit theory, we mapped potential habitat networks in the Guangdong-Hong Kong-Macao Greater Bay Area and projected dynamics under three scenarios: Current Trend Scenario (CTS), Sustainable Development Scenario (SDS), and Ecological Protection Scenario (EPS) for 2030-2070. Each scenario included two sub-scenarios to compare climate change and land-use effects. Results show that EPS initially expands habitat network over a short period but declines thereafter; SDS shows a steady decline throughout the projection period; and CTS generates the most severe habitat loss. Comparison of sub-scenarios revealed that land-use change influences climate impacts based on development pathways. Under EPS and SDS, incorporating land-use change enhanced habitat connectivity in early decades, whereas under CTS, land-use change consistently accelerated habitat loss. Our findings reveal that climate and land-use change jointly drive irreversible degradation of shorebird habitat networks, characterized by patch loss, corridor simplification, and network collapse. While ecologically oriented land-use can slow this trajectory and sustain connectivity in the short term, it cannot offset long-term climate pressures. This demonstrates the need for more ambitious conservation measures that integrate climate mitigation and land-use adaptation to sustain habitat networks under global change.

1. Introduction

Migratory waterbirds, particularly shorebirds (Charadriidae and Scolopacidae), preferentially utilize habitat edges along inland and coastal waters and rely heavily on interconnected habitat networks for foraging and stopovers (Zockler et al., 2016; Ma et al., 2023; Gallo-Cajiao et al., 2024). Their sensitivity to changes in habitat connectivity and rapid response to environmental disturbances make them effective bioindicators of coastal ecosystem health (Ross-Smith et al., 2016; Yoon et al., 2018; Li et al., 2024). However, the integrity of these habitats is severely threatened by converging global change

stressors. Accelerated urbanization, large-scale land reclamation, and infrastructure development have collectively led to the widespread loss and fragmentation of coastal wetlands, thereby threatening the integrity of shorebird habitats (Mott et al., 2023; Liu and Ma, 2024). Hard engineering measures such as seawalls and dikes enforce coastal squeeze, hindering the inland migration of tidal flats and salt marshes, intensifying habitat loss under sea-level rise scenarios (Nazarnia et al., 2020). Meanwhile, climate change exacerbates these pressures by altering temperature and precipitation patterns, disrupting food resource availability and creating phenological mismatches between shorebirds and their prey (Breiner et al., 2022; Wang et al., 2022). These stressors

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underscore the critical need for a comprehensive framework to identify and manage key shorebird habitats.

Given the spatially dynamic nature of migratory shorebird ecology, identifying and managing functional habitat networks is essential for effective conservation planning (Huang et al., 2025). In migratory systems, the ecological value of a habitat patch depends not only on its local suitability, but also on how it is connected to other stopover, foraging, and roosting sites across the landscape (Lisovski et al., 2024; Peng et al., 2025). In this context, the structural integrity and functional cohesion of the network, reflected in the degree of connectivity among habitat patches, are primary determinants of migratory success and long-term population viability (de Felipe et al., 2024; Lisovski et al., 2024). Crucially, while research on habitat area loss is abundant, a significant knowledge gap remains regarding the systematic understanding of the complex interactive and compounding effects of future climate change and urban development on network connectivity (Hoffmann et al., 2019; Morelli et al., 2020; Lin et al., 2026). Most existing studies still focus on single drivers or treat them in aggregate, which can obscure the specific pathways through which habitat degradation and fragmentation occur (Liu et al., 2024b; Wei et al., 2024). Furthermore, established conservation efforts, such as the *Action Plan for the Protection and Restoration of Migratory Bird Flyways in China (2024–2030)*, often remain focused on fixed Protected Areas (PAs), failing to adequately address the need for robust, dynamic, and functional corridors across landscapes (Delach et al., 2024).

The Guangdong-Hong Kong-Macao Greater Bay Area (GBA) provides a representative case for examining how climate change and rapid urban development reshape shorebird habitat network connectivity. As an irreplaceable stopover region for migratory waterbirds along the East Asian-Australasian Flyway (EAAF), the GBA supports diverse wetland habitats, including extensive mudflats, mangroves, estuaries, and aquaculture ponds, which sustain important waterbird populations (Zhang et al., 2019; Ye et al., 2025). However, over the past four decades, the region has faced unprecedented competition for land and sea resources (Lin et al., 2025), and the coastal habitats supporting these migratory waterbirds have become increasingly threatened by multiple pressures, including land reclamation, urban expansion, and climate-induced coastal degradation (Wikramanayake et al., 2020). This combination of pressures means that the future of the GBA's ecologically sensitive coastal areas is closely tied to regional policy and spatial planning. Translating global strategic goals, such as the Kunming-Montreal Global Biodiversity Framework (KMGBF) target of establishing well-connected and resilient ecosystems, into actionable outcomes in the GBA requires a detailed, scenario-based understanding of how land-use trajectories may mediate or intensify climate impacts on ecological connectivity (Gurney et al., 2023; Spiliopoulou et al., 2023). Addressing this challenge requires robust spatial modeling that can anticipate changes in network function and prioritize zones that can serve as resilience-based refugia under future stress (Stralberg et al., 2020; Liang et al., 2024; Xu et al., 2024a; Su et al., 2025).

To address this critical gap, this study establishes a robust framework to explore the future dynamics of shorebird habitat networks in the GBA under multiple development and climate scenarios. Our study provides two primary innovations to the field by: (1) disentangling coupled impacts on connectivity. We employ scenario-specific sub-scenarios to explicitly isolate and quantify the modulating role of contrasting future land-use pathways on the projected effects of climate change on habitat network functionality and resistance; (2) policy-relevant resilience assessment. We apply a comprehensive connectivity assessment to a high-pressure coastal system under three distinct, policy-relevant future pathways (Current Trend, Sustainable Development, and Ecological Protection). This provides policymakers with directly comparable, long-term projections of ecological network resilience that are essential for proactive spatial planning.

Specifically, our research has three main objectives: (1) to identify and delineate the potential shorebird habitat network using Species

Distribution Models and Circuit Theory; (2) to assess how the structural and functional integrity of this network changes under multiple, policy-relevant land-use and climate scenarios spanning 2030–2070; and (3) to quantify the independent and combined contributions of climate change and land-use transformation to future habitat connectivity loss. Ultimately, our findings offer scenario-specific and actionable scientific guidance for strengthening the GBA's ecological security pattern and ensuring alignment with global conservation commitments.

2. Materials and methods

2.1. Study area

The GBA, located in southern China at the lower reaches of the Pearl River and bordering the South China Sea, covers approximately 56,000 square kilometers. Although it accounts for only 0.6% of China's land area, it supports a human population of approximately 86.7 million. In 2023, the region's GDP exceeded 14 trillion RMB, making it one of the most urbanized bay areas in the world and ranking fourth globally after the New York, San Francisco, and Tokyo Bay Areas (Yang et al., 2019). The region contains four Ramsar-designated wetlands of international importance, providing critical stopover sites for shorebirds (Yang et al., 2022).

Meanwhile, the coastal region of the GBA is subject to significantly greater climate change pressure than inland provinces (Jiang et al., 2024). Over the past 60 years, the region has experienced an average temperature increase of 0.21 °C per decade, accompanied by more intense and concentrated rainfall, an increasing number of heavy precipitation days, and a sea-level rise rate that exceeds the national average (Xin et al., 2021).

Our study area includes nine coastal cities, incorporating a 10-km seaward buffer zone to account for coastal and nearshore ecological processes (Fig. 1).

2.2. Methodological framework and scenario settings

This study developed a scenario-based framework to identify potential habitat networks for shorebirds (Fig. 2). First, habitat suitability across the study area was modeled using Maximum Entropy (MaxEnt), followed by the delineation of core habitat patches via Morphological Spatial Pattern Analysis (MSPA) and related spatial methods. Subsequently, a resistance surface for shorebird migration was constructed using Spatial Principal Component Analysis (SPCA), and habitat corridors connecting the core patches were identified based on circuit theory. By integrating habitat patches and corridors under different scenarios, we delineated potential habitat networks.

To account for the dual pressures of climate change and land-use transitions, we designed three scenarios for simulation: the Current Trend Scenario (CTS), the Sustainable Development Scenario (SDS), and the Ecological Protection Scenario (EPS). EPS aligns with SSP1-RCP2.6, representing a pathway emphasizing strong ecological protection and low emissions; SDS corresponds to SSP2-RCP4.5, reflecting a balanced trajectory between development and conservation; and CTS parallels SSP5-RCP8.5, depicting a future dominated by rapid economic growth and limited environmental safeguards. To examine long-term dynamics, we conducted simulations for the years 2030, 2050, and 2070. These scenarios were designed to represent contrasting policy-relevant development and conservation pathways, thereby enabling comparison of how alternative planning orientations may influence future habitat network dynamics (Table A1).

To further disentangle the respective impacts of climate and land-use change, each scenario includes two sub-scenarios: Sub-scenario I, serving as the integrated scenario, considers simultaneous changes in both climate and land use. In contrast, Sub-scenario II, as the climate-driven scenario, serves as a control condition, isolating the effect of climate change by keeping land-use variables constant (Details are

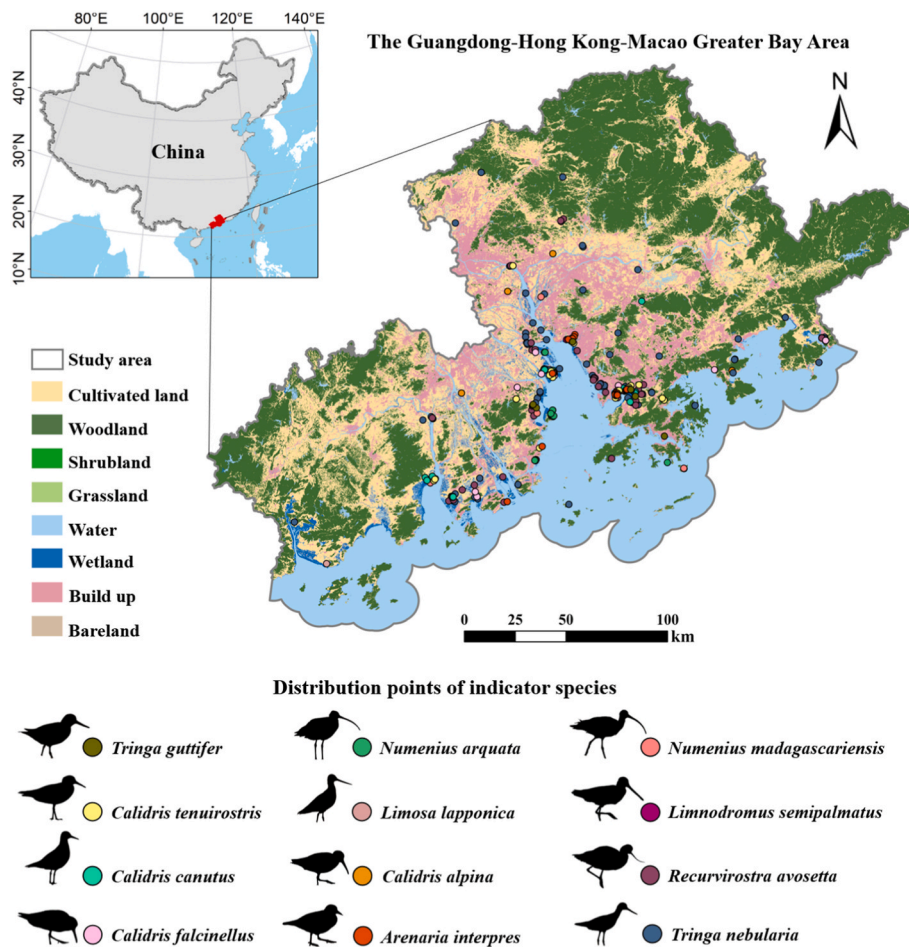


Fig. 1. Geographical location and land use/cover of the study area.

provided in Appendix A.1).

In the real world, climate and land-use changes are intrinsically coupled and cannot be physically separated. Sub-scenario II is a theoretical construct designed to isolate and quantify the influence of contrasting land-use pathways on connectivity by holding land-use variables constant relative to the coupled scenario setting. This comparison allows us to evaluate how alternative planning orientations may mediate climate-related impacts on habitat network dynamics. Accordingly, Sub-scenario I (Coupled Impacts) represents the primary modeled projection under the adopted scenario assumptions, whereas Sub-scenario II provides a comparative reference for interpreting the potential contribution of land-use pathways.

2.3. Data sources and preprocessing

This study primarily utilized three types of data: shorebird occurrence data, climate change data, and geospatial data.

Species occurrence data were compiled from our team's field surveys and citizen science databases. During 2020–2022, our team participated in the Nationwide Synchronized Surveys of Coastal Waterbirds. A combination of transect and point count methods was employed, whereby birds were observed and counted from fixed high vantage points near open water bodies or extensive mudflats to ensure full visibility of habitats and improve counting accuracy. In total, 53 field surveys were conducted, resulting in the collection of 1426 shorebird occurrence records across the GBA. Publicly available records from the China Bird Report Center website (<http://www.birdreport.cn/>), eBird (<https://ebird.org>) and the Global Biodiversity Information Facility (<https://www.gbif.org>) were also compiled for the same time period to

ensure temporal compatibility with the field survey data.

Climate data were obtained from the WorldClim v2.1 database, which includes 19 bioclimatic variables related to temperature and precipitation. These data cover both current climatic conditions and three future scenarios: SSP1-RCP2.6, SSP2-RCP4.5, and SSP5-RCP8.5. For each variable, the downscaled CMIP6 GeoTIFF files were used. Geospatial datasets included eight variables such as land use, vegetation, and topography, as detailed in Table 1. Considering the importance of land-use change for future projections, this study employed the Finer Resolution Observation and Monitoring of Global Land Cover (FROM-GLC Simulation) dataset, which provides high-resolution projections of global land-use change under various pathway scenarios. To ensure its accuracy and applicability to our study area, we manually calibrated the dataset based on local conditions. Specifically, we visually compared the simulated land-use patterns with recent Landsat 8 satellite imagery to assess consistency with real-world observations. We further validated the reliability of the projected land-use boundaries under future sea-level-rise scenarios using the flood-inundation analysis tool within ArcGIS Pro's hydrologic modeling framework. Detailed results of sea-level rise inundation are provided in Appendix A.3. These steps improved the reliability and applicability of the dataset for subsequent simulations and projections.

We used a scoring system to select indicative shorebird species that are common, migratory, and sensitive to habitat change along the East Asian-Australasian Flyway (EAAF) in the GBA (Huang et al., 2025). Detailed scoring criteria and species information are provided in Appendix A.2. Ultimately, 12 indicator species were identified, including 10 threatened species (IUCN, 2025). Despite inter-species differences, they share critical non-breeding habitat functions during stopover,

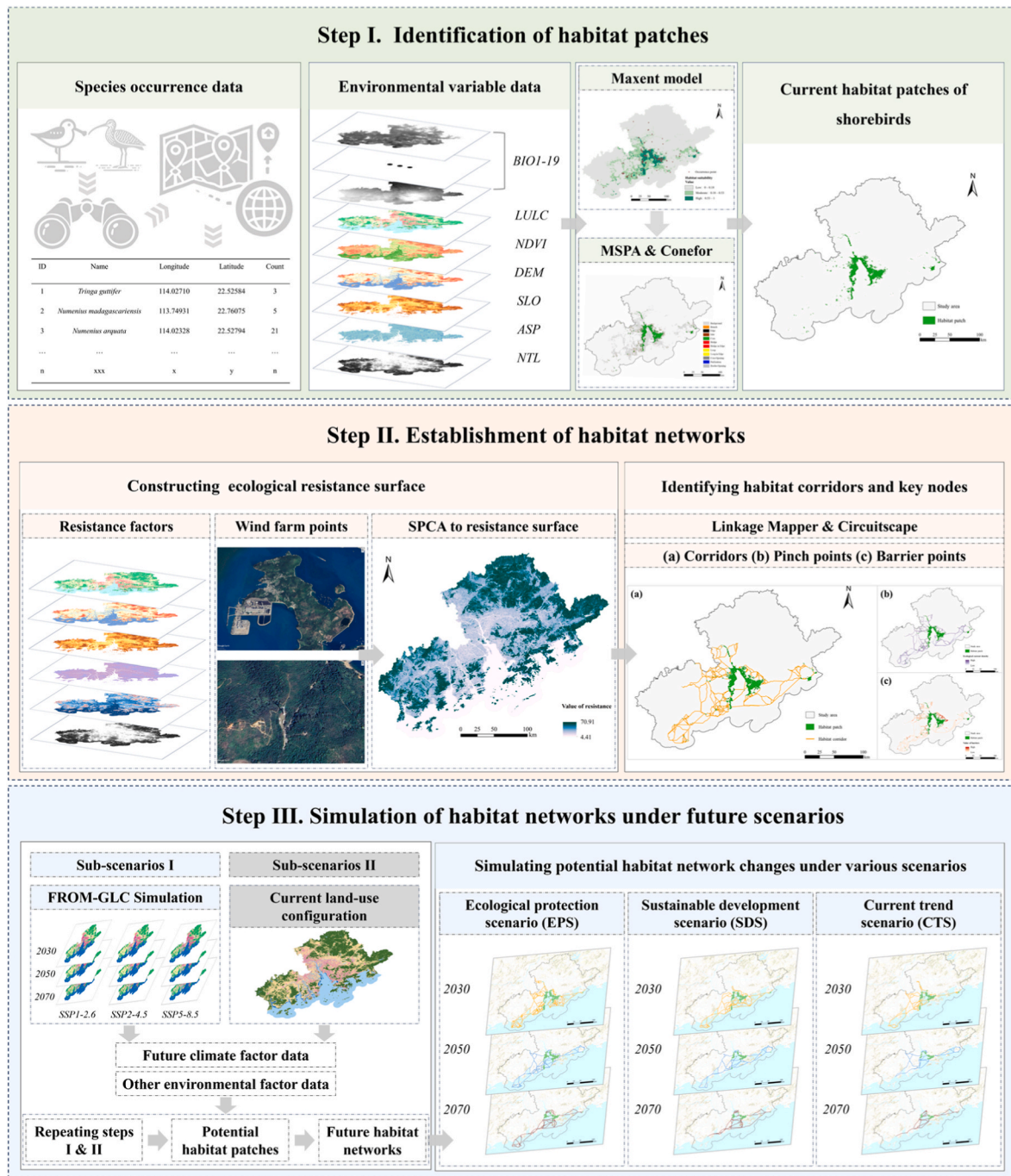


Fig. 2. The methodological framework of this study.

predominantly relying on functionally similar habitat types such as intertidal mudflats, shallow water areas, and associated aquaculture ponds. Modeling the species as a functional group helps mitigate the issue of sparse occurrence data (especially after spatial thinning) which could otherwise lead to model over-fitting and reduced predictive power for individual rare species. The resulting multi-species suitability map characterizes the potential habitat network for migratory shorebirds.

To mitigate spatial autocorrelation and sampling bias, the integrated occurrence dataset was subjected to spatial thinning, removing all records closer than 1 km. This resulted in a final sample size of 337 independent occurrence points used for MaxEnt modeling.

2.4. Identification of habitat patches

Data pre- and post-processing were performed in the R statistical environment (R version 4.3.2), utilizing packages including ENMeval, dismo, and raster (Muscarella et al., 2014; Hijmans et al., 2024). Environmental variables included 19 bioclimatic variables and six geospatial variables, namely land use, vegetation, altitude, slope, aspect, and nighttime lights (Table A4). All variables were standardized and resampled to 30×30 m using the nearest-neighbor interpolation method. Since multicollinearity can lead to unstable parameter estimates in SDMs (Sillero, 2011), we screened the environmental variables to reduce the negative impact of multicollinearity. Then we calculated Pearson's correlation coefficients among all environmental variables. For variables with $|r| \geq 0.85$, we removed them based on ecological

Table 1

Data sources and description in this study.

Data	Sources	Description
Climate data (BIO1-19)	WorldClim database (http://www.worldclim.org/)	Raster, 1 km × 1 km
Land-use/land-cover (LULC)	Annual China Land Cover Dataset (http://doi.org/10.5281/zenodo.4417809)	Raster, 30 m × 30 m (2022)
	Finer Resolution Observation and Monitoring of Global Land Cover dataset (http://www.geodata.cn)	Raster, 30 m × 30 m (2030, 2050, 2070)
Digital Elevation Model (DEM)	Geographic Spatial Data Cloud (https://www.gscloud.cn/)	Raster, 30 m × 30 m (2022)
Slope (SLO)	Calculated from DEM data in ArcGIS Pro	Raster, 30 m × 30 m (2022)
Aspect (ASP)	Calculated from DEM data in ArcGIS Pro	Raster, 30 m × 30 m (2022)
Terrain Ruggedness Index (TRI)	Calculated from DEM data in ArcGIS Pro	Raster, 30 m × 30 m (2022)
Local Deviation from Global Mean (LDFG)	Calculated from DEM data in ArcGIS Pro	Raster, 30 m × 30 m (2022)
Normalized differential vegetation index (NDVI)	Landsat 8 Surface Reflectance NDVI (2022) Dataset, Calculated Using the Google Earth Engine Platform	Raster, 30 m × 30 m (2022)
Nighttime Light index (NTL)	NOAA VIIRS DNB Monthly V1 (2022) dataset, calculated using the Google Earth Engine platform	Raster, spatially enhanced using bilinear interpolation to a resolution of 30 m × 30 m (2022)

relevance and contribution rates.

In Sub-scenario I, both future bioclimatic variables and projected land-use datasets were incorporated, reflecting simultaneous changes in climate and land-use patterns. In contrast, Sub-scenario II used the same set of future bioclimatic variables, while land-use variables remained unchanged, allowing only bioclimatic variables to vary. The distribution records of the indicator species, along with the selected environmental variables, were input into MaxEnt software (version 3.4.4) for species distribution modeling. 75% of the occurrence data were randomly selected for model training, with the remaining 25% reserved for testing. The model was run using the bootstrap method with 10 replicates, and the average output was used as the final prediction. The output format was set to Logistic, while all other parameters remained at their default settings. To evaluate the relative importance and contributions of environmental variables, the jackknife test was applied. The habitat suitability maps produced by the MaxEnt model were converted into binary maps to identify the suitable habitats.

Based on these suitable habitats, we further identified the habitat patches to serve as network nodes by integrating MSPA and landscape connectivity metrics. MSPA was used to extract core habitats, which represent larger habitat patches within the foreground pixels that can provide extensive habitats for species and are important for biodiversity conservation. We then applied Conefor 2.6 to calculate the Probability of Connectivity (PC) index and the delta Probability of Connectivity (dPC), as detailed in Appendix A.5. Patches larger than 10 ha were considered critical for maintaining bird diversity (Chen et al., 2024). Finally, only those patches that were identified as core areas by MSPA and had dPC >1 were designated as shorebird habitat patches (Saura and Torné, 2009).

2.5. Identification of habitat corridors

2.5.1. Evaluation of the ecological resistance surface

In this study, the ecological resistance surface was developed by combining seven environmental and anthropogenic factors weighted

through SPCA. Coastal wetland shorebirds are influenced by both environmental and anthropogenic factors. Land-use is a major driving factor (Patankar et al., 2021), with shorebirds favoring specific habitats such as reed beaches, bare flats, grasslands, and wetlands, which offer abundant foraging opportunities. Vegetation cover, as indicated by NDVI, is a key factor influencing waterbird distribution due to its close association with foraging habitats and food resources (Barchiesi et al., 2022). For shorebirds, areas with lower coastal vegetation cover are preferred, as these regions provide abundant benthic food resources (Ma et al., 2013). Topographic features, such as elevation and slope, also impact shorebird habitat suitability (Zockler et al., 2016); shorebirds generally prefer low-elevation, flat areas, while elevated and rugged terrain can hinder their normal activities. Local Deviation from Global Mean (LDFG) and Terrain Ruggedness Index (TRI) were also included as resistance factors for shorebirds (Wang et al., 2021). Detailed descriptions of these indices and their relevance to shorebirds, along with the formulas used for their calculation, are provided in Appendix A.6. Most previous studies have determined the weights of these factors using methods such as the Analytic Hierarchy Process (AHP). These methods typically rely on expert judgment to assign scores and derive weights, which can introduce a high degree of subjectivity (Liu et al., 2024a). In contrast, we applied SPCA to incorporate spatial data information (Harris et al., 2011). We performed Z-score standardization on the resistance factor raster data, followed by the application of the Principal Components tool in ArcGIS Pro (Table A5).

Wind farms can affect migratory birds through several mechanisms (Marques et al., 2014). Research shows that the rotation of turbine blades and signal lights can disrupt shorebird habitats and migratory paths, impacting ecological structure and stability (Madsen and Boertmann, 2008; Cohen et al., 2022). Habitat alteration and fragmentation may reduce habitat suitability and resource availability near turbines (Tolvanen et al., 2023). Disturbances caused by rotor movement, noise, vibration, flashing lights, and human activities can lead to behavioral changes, such as avoidance or altered migratory routes (Drewitt and Langston, 2006; Marques et al., 2020, 2021). We extracted the offshore and onshore coordinates of wind farm locations in the study area from the Vortex Interface (vortexfd.com) and applied 500 m buffer zones around these points in ArcGIS Pro. These areas were considered high-resistance zones and spatially overlaid with the raster data generated from SPCA, resulting in the final resistance surface layer.

2.5.2. Establishment of habitat corridors

Circuit theory is commonly used to model habitat corridors by estimating resistance distances and identifying key areas that facilitate species movement. Areas with the highest 'current' density are recognized as migration hotspots, highlighting their critical role in maintaining landscape connectivity. In this study, habitat corridors were extracted using the Linkage Mapper Toolbox and Circuitscape software. The Centrality Mapper module was employed to assess the importance indices of habitat patches and corridors. Additionally, the Pinch Point Mapper and Barrier Mapper modules were used to identify ecological pinch points and barriers within the corridors. Using the natural breaks classification method, the top 20% of areas with the highest current density were extracted as ecological pinch points, while the top 20% of areas with the highest resistance values were identified as ecological barriers (Huang et al., 2025). Ecological pinch points, characterized by high current density, represent areas with limited alternative pathways and therefore require priority protection to ensure habitat conservation. Ecological barrier points, on the other hand, obstruct species movement between habitats, and their mitigation is essential for improving overall network connectivity.

2.6. Evaluation of habitat network

Based on complex network theory, habitat patches are regarded as network nodes, and habitat corridors are treated as network edges. The

evaluation of ecological network nodes is conducted through metrics such as degree, clustering coefficient, betweenness centrality, closeness centrality, and eigenvector centrality. Degree represents a node's direct connectivity, identifying highly connected ecological patches that facilitate species movement. Clustering coefficient reflects local stability, where tightly connected neighboring patches enhance habitat resilience. Betweenness centrality highlights key bridge nodes that maintain migration pathways and mitigate fragmentation. Closeness centrality measures a node's global efficiency in species dispersal, identifying critical diffusion hubs. Eigenvector centrality assesses a node's influence within the network, emphasizing patches with widespread ecological impact through connections to other significant habitats.

Subsequently, the ecological network connectivity index is applied to assess the connectivity of the habitat network (Santini et al., 2016; Zhao et al., 2024). This index, comprising the network loop degree (α), node connectivity rate (β), network connectivity degree (γ), and connectivity density index (ρ) analyzes changes in network connectivity (Details are provided in Appendix A.7). It provides a comprehensive evaluation of overall ecological network connectivity using single indicators.

The detailed process and results of the potential spatial configuration of the shorebird habitat network are provided in Appendix A.8.

3. Results

3.1. Changes in habitat patches under different scenarios

The baseline potential suitable habitat in the GBA consists of 232 discrete patches covering 1629 km². Large patches form continuous complexes along the coast and riparian corridors beside the Pearl River,

while smaller patches occur inland and within urban zones where fragmentation is severe (Fig. 3a). Under the integrated climate and land-use trajectory (Sub-scenario I), our projections showed that EPS initially expanded habitat extent. Both patch count and total area increased through 2030, reaching 245 patches and 1764 km² respectively, before declining after 2050. In contrast, the SDS drove steady decline throughout the projection period, with patch numbers decreasing to 179 and total area contracting to 1418 km² by 2050. CTS produced the most severe habitat loss, reducing patches to 117 and area to 1224 km² by 2070. These trajectories confirm that only EPS provided a temporary, short-term habitat expansion, while both SDS and CTS resulted in continued fragmentation and loss (Fig. 3b). Moreover, the spatial changes are accompanied by a consistent northward shift in the average latitude of the remaining habitat patches (Fig. 3c and Fig. A10). This latitudinal redistribution reflects the influence of rising temperatures and sea-level encroachment, which progressively reduce habitat suitability in low-latitude coastal zones.

Comparing Sub-scenario II with Sub-scenario I revealed how land-use change could either mitigate or amplify climate impacts (Fig. 3b). Under EPS, Sub-scenario II produced smaller initial gains than the integrated scenario, with both trajectories declining after mid-century. This pattern indicated that land-use change initially enhanced habitat gains beyond those achieved through climate factors alone. Under SDS, land-use dynamics partially offset climate-driven losses in patch count while marginally reducing total area. Conversely, under CTS, incorporating land-use change accelerated habitat decline, amplifying losses in both patch number and total area by 2030. These contrasts demonstrate that land-use change may buffer or exacerbate climate-driven habitat trends depending on the development pathway. The results highlight the importance of coupling emissions reductions with targeted land-use

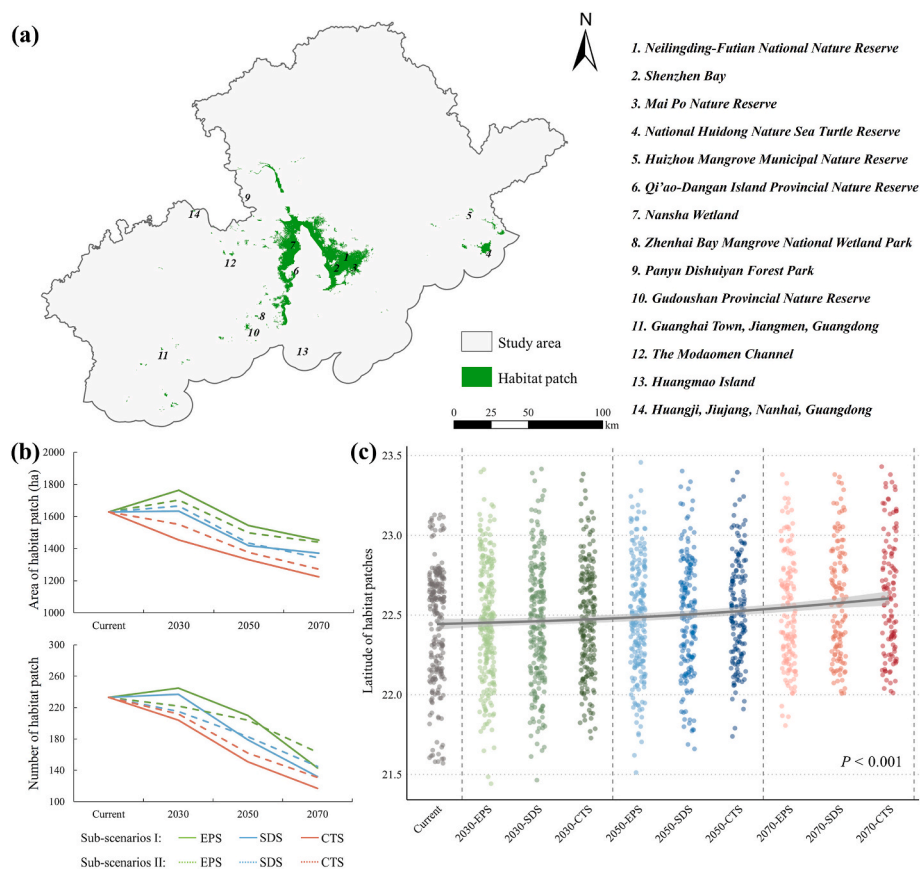


Fig. 3. (a) Potential shorebird habitat patches identified in the study area and PAs listed in the “Action Plan for the Protection and Restoration of Migratory Bird Flyways in China (2024–2030)”. (b) Changes in the number and area of habitat patches under different scenarios. (c) Spatial variations in the distribution of habitat patches under Sub-scenario I.

management to optimize shorebird habitat conservation.

To better understand habitat persistence and resilience, we further analyzed the proportion of stable habitat patches, defined as those consistently identified as suitable in both current and future periods. The results reveal a continuous decline over time under the combined impacts of climate change and land-use transitions (Fig. 4). In the short term, EPS maintains a relatively high retention rate. However, after 2050, the degradation of stable habitats becomes more pronounced. By 2070, this proportion drops to 54.94 percent under EPS, 46.63 percent under SDS, and further declines to 42.47 percent under CTS. Spatially, stable patches are predominantly concentrated in estuarine and protected coastal zones. Notable examples include the Nansha Wetland, the Futian Mangrove National Nature Reserve, and the Mai Po and Inner Deep Bay wetlands, which collectively sustain large and persistent shorebird habitats. These patches function as critical nodes for maintaining migratory stopover, foraging, and roosting functions within the habitat network. In contrast, many smaller patches along the open coastline have undergone progressive degradation and disappearance, particularly under CTS, as intensified land conversion and sea-level rise

increasingly undermine the suitability of low-lying intertidal zones for shorebird use.

3.2. Changes in habitat corridors under different scenarios

The potential shorebird habitat network in the GBA relies on 489 ecological corridors spanning 3729.7 km. The longest corridor runs 86.5 km, connecting the Tan River and Yamen Watercourse while linking key sites like the Gudoushan Provincial Nature Reserve and the Modaomen Channel. These corridors provide the basic framework for the regional habitat network, allowing shorebirds to move across fragmented coastal landscapes (Fig. 5a). Under the integrated climate and land-use trajectory (Sub-scenario I), connectivity grows during the early EPS period. Corridor count and total length peak at 536 and 3815.1 km by 2030. This trend shifts after mid-century by 2070 both measures drop significantly to 263 corridors and 1896.1 km. SDS shows a similar pattern but declines more gradually, ending with 237 corridors and 1840.2 km in 2070. CTS demonstrates continuous losses throughout the century, shrinking the network to 197 corridors and 1592.3 km by 2070.

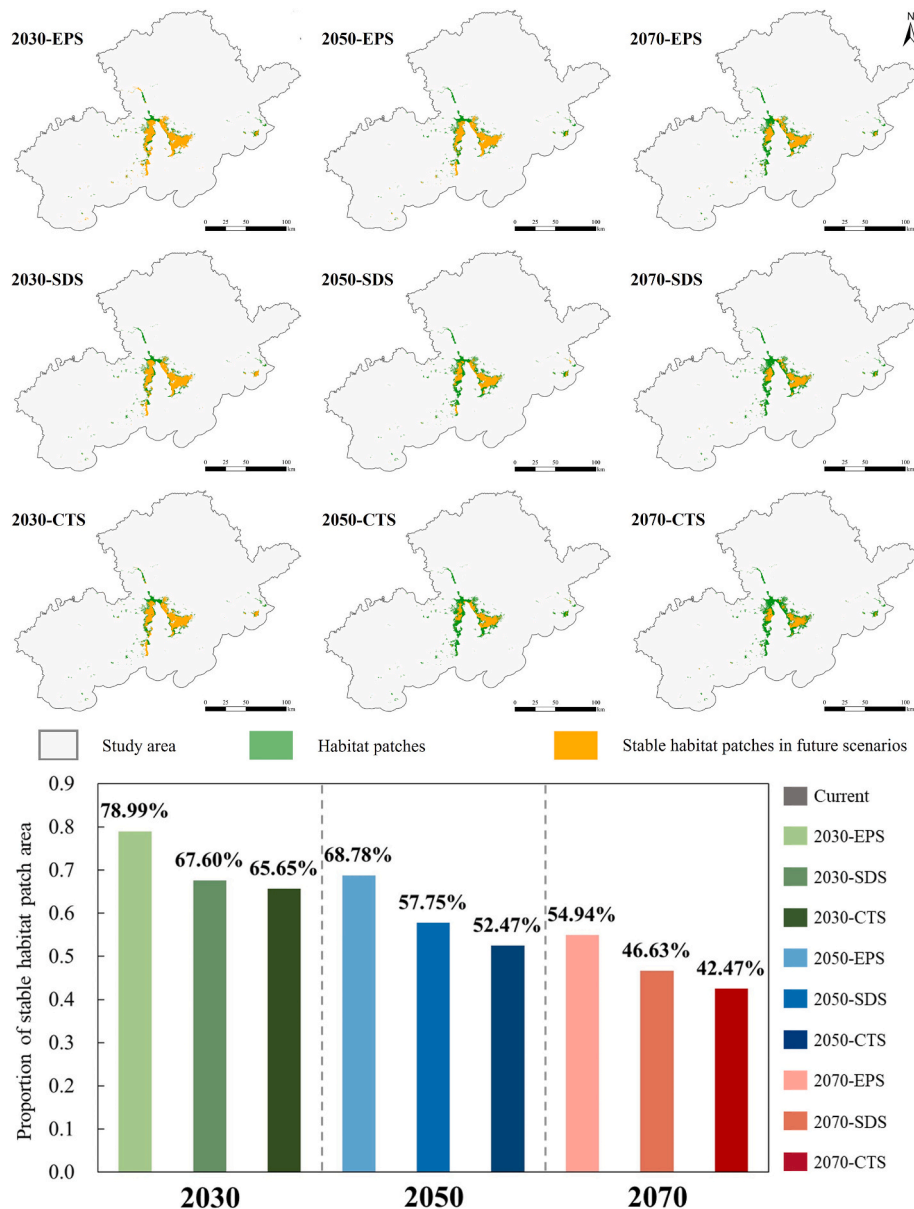


Fig. 4. Spatial distribution of stable habitat patches and proportion of stable habitat patch area.

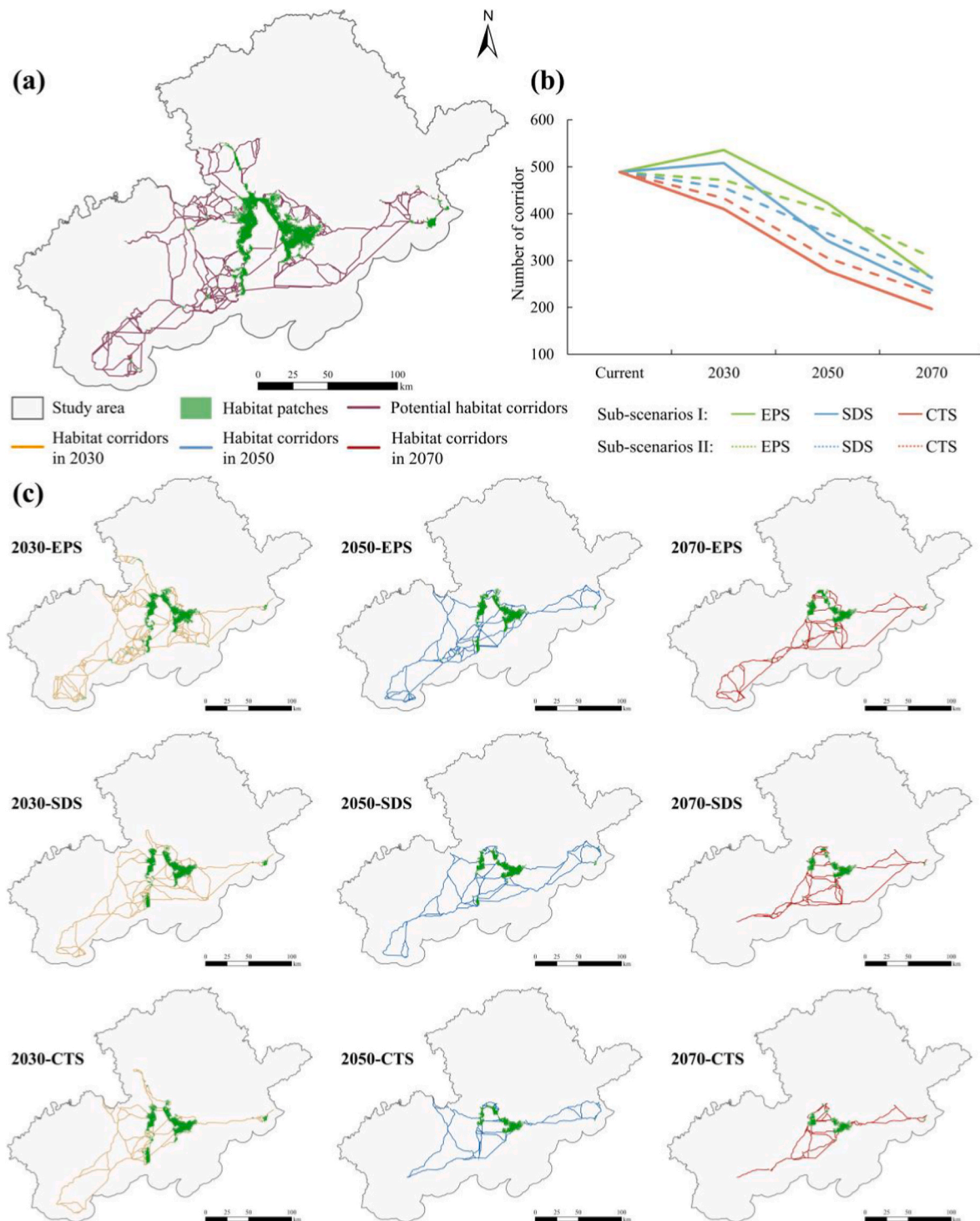


Fig. 5. (a) The establishment results of potential habitat corridors. (b) Changes in the number of habitat corridors under different scenarios. (c) Spatial distribution of habitat corridors under different scenarios.

In general, EPS delivers short-term gains but cannot fully offset long-term pressures from climate and land-use changes. SDS maintains moderate connectivity, while CTS leads to severe fragmentation and network breakdown (Fig. 5b). Notably, several important corridors persist across different timeframes and scenarios. These include connections between the National Huidong Sea Turtle Nature Reserve and Mai Po Nature Reserve, Shenzhen Bay and Qi'ao-Dangan Island, and Zhenhai Bay Mangrove National Wetland Park and Guanghai Town in Jiangmen (Fig. 5c and Fig. A11).

Comparison of Sub-scenario II with Sub-scenario I reveals that land-use change alters connectivity in different ways depending on the development pathway. Under EPS and SDS, the inclusion of land-use dynamics in Sub-scenario I leads to the formation of additional corridors during the early decades, with numbers and lengths exceeding those under climate-only projections in 2030. For instance, EPS shows 536 corridors under Sub-scenario I, compared to 472 under Sub-scenario II. This suggests that ecologically oriented land-use can initially enhance habitat connectivity. However, by 2070, climate-only projections retain

higher corridor numbers and longer total lengths, as land-use expansion in Sub-scenario I gradually weakens the network. Under CTS, land-use change accelerates connectivity loss across all decades, limiting potential movement routes for shorebirds. These findings show that while land-use management may provide early benefits, only sustained ecological protection can prevent long-term habitat isolation and connectivity loss under climate change and sea-level rise.

3.3. Evaluation and comparison of habitat networks under different scenarios

Across all scenarios, the ecological network connectivity index α , β , and γ exhibit a general downward trend over time, indicating progressive simplification and fragmentation of the network (Fig. 6a). EPS and SDS consistently outperform CTS in maintaining network integrity, particularly in the short term. For instance, under Sub-scenario I, α reaches 0.602 in EPS by 2030 and 0.580 in SDS, compared to 0.514 in CTS. Similarly, β and γ attain higher values in EPS (2.188 and 0.735, respectively), reflecting better-connected and more cohesive networks. However, this advantage diminishes over time. By 2070, all indices decline substantially, with CTS showing the most severe degradation ($\alpha = 0.354$, $\beta = 1.684$, $\gamma = 0.571$ in Sub-scenario I).

The impact of land-use change, when compared to climate drivers alone, varies across scenarios and periods (Fig. 6b). In EPS, the inclusion of land-use change initially enhances α by 5.3% in 2030, suggesting a short-term synergistic effect between ecological planning and climate adaptation. However, this benefit reverses by 2070, when α drops by 4.7% relative to the climate-only projection. In contrast, SDS and CTS

show consistent negative effects of land-use change on all indices throughout the projection period. In 2070, CTS exhibits the steepest decline in α (−9.1%), β (−4.1%), and γ (−3.9%) under Sub-scenario I compared to Sub-scenario II, highlighting the compounding impact of unregulated land-use expansion under high-emission pathways. Overall, the habitat network is undergoing a process of simplification. Under CTS, network structures are becoming increasingly fragmented, with both habitat patches and corridors shrinking in spatial extent and functional capacity. Local subnetworks, particularly in the southern region where small, fragmented island habitats are located, are gradually disappearing. In contrast, some clusters of robust source patches and corridors persist in larger, well-managed coastal wetland areas. Although early improvements are observed under EPS, the long-term trend still indicates a gradual simplification of the network, especially in peripheral zones.

4. Discussion

4.1. Methodological refinement and ecological interpretation of habitat corridors

Numerous studies have shown that habitat networks play an important role in linking fragmented patches, facilitating species movement, and supporting ecological processes (Mossman et al., 2015; Keten et al., 2020). By mitigating the effects of habitat fragmentation, such networks are increasingly regarded as an important tool for biodiversity conservation (Xu et al., 2024b). However, many such studies are primarily rooted in urban planning and landscape ecology,

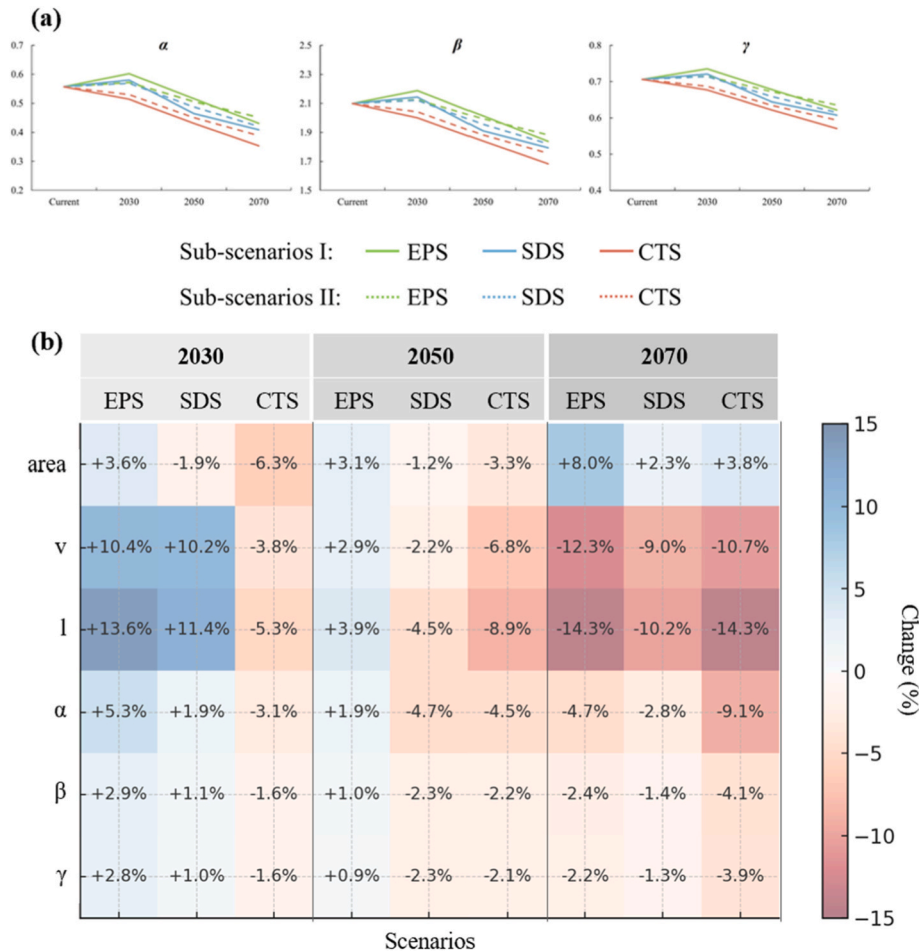


Fig. 6. (a) The ecological network connectivity index under different scenarios. (b) Relative changes in habitat network metrics under Sub-scenarios I compared to Sub-scenarios II.

and often lack integration of species-specific ecological information, which may limit their value for biodiversity conservation (Ashrafzadeh et al., 2020; Modica et al., 2021; Beger et al., 2022; Mu et al., 2024). In this study, we addressed this limitation by focusing on shorebirds as indicator species and by integrating habitat preferences and migratory behavior into both habitat suitability modeling and resistance surface construction.

The resulting pattern of habitat nodes and corridors supports the ecological relevance of this framework. High-centrality habitat nodes and corridors, such as the complex formed by the Futian Mangrove National Nature Reserve and Mai Po wetlands, were consistently identified as key components of the regional network. Moving beyond generic landscape ecology approaches, our study improved the ecological relevance of resistance surface construction by integrating shorebird migratory behavior and habitat preferences, rather than relying solely on expert judgment. The application of Spatial Principal Component Analysis (SPCA) further improved the objectivity of the resistance surface and enabled a more realistic representation of multiple environmental constraints (Liu et al., 2024a). In addition, the coastal wind farms identified in our analysis may act as local resistance sources, reinforcing the need to avoid such infrastructure in ecologically sensitive areas and to strengthen post-construction monitoring (Guan, 2023).

The modeled potential habitat network also showed broad consistency with existing conservation planning and regional knowledge in the GBA (Yang et al., 2022, 2024; Liu et al., 2025). The identified potential habitat patches overlapped with existing Protected Areas listed in the *Action Plan for the Protection and Restoration of Migratory Bird Flyways in China (2024-2030)*, including several well-recognized waterbird habitats in the GBA (Fig. 3a). Similarly, the corridor pattern identified in our study was broadly consistent with the regional corridor framework proposed in the *Pearl River Delta Waterbird Ecological Corridor Construction Plan (2020-2025)* issued by the Forestry Administration of Guangdong Province. Although these consistencies do not constitute direct validation of observed migration routes, they provide indirect support for the ecological plausibility and policy relevance of our modeling framework.

The ecological pinch points and barriers identified through circuit theory highlight priority areas for targeted restoration within the potential habitat network. Transitional zones at the interface of urban and natural landscapes are especially critical for sustaining corridor connectivity and ecological functionality. To simultaneously mitigate ecological barriers and prevent further degradation of pinch points, cities should adopt integrated landscape management strategies that prioritize the planning and implementation of blue-green infrastructure. Priority actions include restoring degraded intertidal flats and estuarine margins, protecting remaining coastal buffer zones, enhancing wetland-urban transition habitats, and integrating ecological corridors into coastal development and zoning plans. These strategies should also incorporate targeted hydrological management and the retention of native vegetation to improve the resilience, continuity, and multifunctionality of urban coastal ecosystems.

4.2. Adaptive strategies for shorebird conservation and habitat network enhancement under future scenarios

Our scenario analysis clearly demonstrates that the GBA's extensive regional development policies (Chong and Pan, 2020), while driving economic growth, have simultaneously contributed to land-use fragmentation (Zhang et al., 2023). Under the development-first CTS trajectory, we project the progressive degradation and eventual functional collapse of the coastal habitat network due to the compounded effects of land-use intensification and climate drivers. This confirms the urgent need to reconcile urban expansion with long-term ecological resilience.

Crucially, the quantified comparison between our sub-scenarios allowed us to distinguish the relative roles of climate change and land-use transformation in shaping connectivity (Baisero et al., 2020).

Notably, in the short term, proactive land-use planning and ecological restoration such as those reflected in EPS can partially offset climate-induced disruptions (α enhanced by 5.3% in 2030), maintaining higher levels of connectivity than under climate change alone. However, this buffering capacity declines over time, particularly under intensifying development trajectories. Unregulated land-use expansion exerts a more immediate and structurally disruptive impact on network integrity (up to 9.1% steeper decline in α under 2070-CTS). These findings underscore the potential of targeted land-use regulation to yield immediate conservation gains, while also emphasizing the importance of prioritizing stable habitat patches that can serve as climate refugia. Such forward-looking planning enhances ecological resilience to future climate-driven pressures. This integrated approach, which jointly considers short-term buffering and long-term structural vulnerabilities, offers a complementary perspective to existing studies that have primarily emphasized synergistic threats in inland systems (Mantyka-Pringle et al., 2015; de Felipe et al., 2024). In contrast, our coastal-focused analysis reveals a temporally lagged but ultimately more profound impact of land-use expansion, which represents a distinction of critical importance for long-term spatial planning.

In this context, greater policy support for biodiversity conservation becomes essential. A representative example is the *Pearl River Delta Waterbird Ecological Corridor Construction Plan (2020-2025)*. Our simulations under EPS and SDS suggest that proactive ecological strategies can reduce habitat loss and fragmentation in the short term. By promoting a more cohesive and resilient habitat network, such corridor-based planning can effectively complement regional development under future environmental change. The findings support established conservation paradigms demonstrating that large, contiguous PAs with targeted waterbird management yield superior biodiversity outcomes (Wauchope et al., 2022). Where the establishment of such PAs is constrained, other effective area-based conservation measures (OECMs) offer viable options for safeguarding ecologically important zones beyond formal PAs boundaries (Brighton et al., 2024). Strengthening the protection and ecological restoration of coastal and island ecosystems is therefore essential for sustaining the regional shorebird habitat network.

Although sites such as the Futian Mangrove National Nature Reserve and Mai Po Nature Reserve have achieved notable conservation gains through focused restoration and adaptive management, our results indicate that several ecologically important shorebird habitats lie outside these well-protected areas. Unprotected intertidal flats, estuarine shorelines and island-associated wetlands constitute the principal conservation gaps within the regional habitat network and are projected to face increasing pressure under future climate and land-use change. Expanding formal protection in these gap areas, upgrading the management of smaller wetland reserves, restoring degraded coastal habitats and more effectively integrating shorebird habitat priorities into regional planning will be critical for maintaining the integrity of the broader shorebird habitat network in the GBA.

In addition to localized efforts, cross-regional collaboration is essential. Facilitating cooperation between inland urban areas and Special Administrative Regions (SARs) can help build a comprehensive conservation network. This is particularly important within the context of EAAF, where recent research emphasizes the importance of improving the social-ecological fit between institutional arrangements and migratory connectivity (Gallo-Cajiao et al., 2024). By strengthening node-level coordination across key flyway sites, conservation planners can more effectively maintain functional connectivity under future scenarios of land-use change and climate pressure. Such coordination enhances the ability of institutions to respond collectively to spatially distributed ecological dynamics across political boundaries. The success of these actions depends on a variety of factors, including hydrological conditions, land-use patterns, population density, and the engagement of local communities and authorities. Financial investment and institutional capacity are equally vital. Targeted support for conservation planning, periodic protection, and adaptive management is critical to

building a climate-resilient wetland network (Kujala et al., 2013). Such a network not only supports shorebird conservation, but also sustains broader biodiversity and human well-being (Assessment, 2005; Gardner and Finlayson, 2018; Breiner et al., 2022).

4.3. Limitations and prospects

Compared to previous studies, this research proposes a framework for analyzing changes in habitat networks under different future scenarios. The framework can be adapted to the specific conditions of different study areas by collecting diverse species distribution data and adjusting key environmental driving factors, thereby positively contributing to biodiversity conservation in various regions. Although we have thoroughly considered the impacts of various environmental factors, such as climate change, land-use change, and sea level rise, on future scenarios, other factors such as Nighttime light, which is influenced by socioeconomic activities, energy use, technological changes, and urbanization pose significant challenges in constructing a comprehensive dynamic prediction model (Kii et al., 2024). Similarly, DEM mainly describes static topographical features, and its changes are influenced by natural and anthropogenic geological processes, the timing and scale of which are difficult to predict accurately. NDVI responses to climate and land-use changes are typically nonlinear and influenced by complex interactions among various factors, making the prediction of future changes highly uncertain (Teng et al., 2023; Mehmood et al., 2024).

The framework proposed in this study is effective for identifying and evaluating modeled potential shorebird habitat networks, but it does not directly represent observed migration routes or species-specific movement pathways. Although the modeled network is broadly consistent with existing important waterbird habitats, Protected Areas, and regional corridor planning in the GBA, these consistencies provide indirect support rather than direct validation. In addition, while the scenario framework was developed under contrasting policy-oriented pathways, current statutory land-use control lines, such as urban development boundaries and ecological protection redlines, were not explicitly imposed as hard spatial constraints in the simulation. Therefore, the results should be interpreted as comparative projections under alternative development and conservation pathways, rather than as exact forecasts under full implementation of existing regulatory boundaries. Obtaining direct observational evidence for target species would require extensive long-term field monitoring and species-specific movement data. Future studies should therefore integrate tracking data, such as GPS or satellite tracking and radio telemetry, and further incorporate policy-constrained land-use simulations to refine the modeled network and improve its applicability to regional conservation planning in densely urbanized coastal regions.

5. Conclusion

This study underscores the critical importance of maintaining habitat corridors to mitigate fragmentation and sustain biodiversity, particularly for migratory shorebirds in densely urbanized coastal regions such as the GBA. By integrating SDMs, landscape connectivity analysis, and circuit theory, and grounding these within a scenario-based framework, we developed a comprehensive approach for identifying and optimizing shorebird habitat networks under current and future scenarios. Scenario-based projections revealed that conservation-oriented development pathways (EPS and SDS) can significantly buffer network degradation and temporarily maintain corridor continuity, yet they remain insufficient to reverse the overarching trajectory of climate-driven habitat decline. Our comparative analysis further demonstrates that unregulated land-use expansion (CTS) exerts the most immediate and structurally disruptive impact, accelerating habitat loss by compounding negative climate effects. These findings highlight the need for ambitious, integrated conservation strategies that combine climate

change adaptation with proactive, policy-relevant land-use planning to preserve coastal biodiversity. Our framework provides a valuable tool for projecting habitat network dynamics and informing conservation planning in coastal regions. Future research should build on these projections by incorporating high-resolution movement data and coastal geomorphological dynamics to refine our understanding of habitat network resilience under accelerating global change.

CRediT authorship contribution statement

Geng Huang: Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Wenjia Hu:** Conceptualization, Methodology, Supervision, Writing – original draft, Writing – review & editing. **Jianguo Du:** Conceptualization, Methodology, Supervision, Writing – review & editing. **Yunzhe Huang:** Investigation, Methodology, Writing – review & editing. **Yifei Jia:** Data curation, Investigation, Project administration, Writing – review & editing. **Yuyu Wang:** Conceptualization, Funding acquisition, Investigation, Project administration, Supervision, Writing – original draft, Writing – review & editing.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.indic.2026.101413>.

Data availability

Data will be made available on request.

References

- Ashrafzadeh, M.R., Khosravi, R., Adibi, M.A., Taktehrani, A., Wan, H.Y., Cushman, S.A., 2020. A multi-scale, multi-species approach for assessing effectiveness of habitat and connectivity conservation for endangered felids. *Biol. Conserv.* 245, 108523.
- Assessment, M.E., 2005. Ecosystems and Human well-being: Wetlands and Water. World Resources Institute.
- Baisero, D., Visconti, P., Pacifici, M., Cimatti, M., Rondinini, C., 2020. Projected global loss of mammal habitat due to land-use and climate change. *One Earth* 2 (6), 578–585.
- Barchiesi, S., Alonso, A., Pazmiño-Hernandez, M., Serrano-Sandí, J.M., Muñoz-Carpena, R., Angelini, C., 2022. Wetland hydropattern and vegetation greenness predict avian populations in Palo verde, Costa Rica. *Ecol. Appl.* 32 (2), e02493.
- Beger, M., Metaxas, A., Balbar, A.C., McGowan, J.A., Daigle, R., Kuempel, C.D., Trembl, E. A., Possingham, H.P., 2022. Demystifying ecological connectivity for actionable spatial conservation planning. *Trends Ecol. Evol.* 37 (12), 1079–1091.
- Breiner, F.T., Anand, M., Butchart, S.H., Flörke, M., Fluet-Chouinard, E., Guisan, A., Hilarides, L., Jones, V.R., Kalyakin, M., Lehner, B., 2022. Setting priorities for climate change adaptation of critical sites in the Africa-Eurasian waterbird flyways. *Glob. Change Biol.* 28 (3), 739–752.

- Brighton, C.H., Massimino, D., Boersch-Supan, P., Barnes, A.E., Martay, B., Bowler, D.E., Hoskins, H.M.J., Pearce-Higgins, J.W., 2024. The benefits of protected areas for bird population trends may depend on their condition. *Biol. Conserv.* 292, 110553.
- Chen, R., Carruthers-Jones, J., Carver, S., Wu, J., 2024. Constructing urban ecological corridors to reflect local species diversity and conservation objectives. *Sci. Total Environ.* 907, 167987.
- Chong, Z., Pan, S., 2020. Understanding the structure and determinants of city network through intra-firm service relationships: the case of Guangdong-Hong Kong-Macao greater Bay area. *Cities* 103, 102738.
- Cohen, E.B., Buler, J.J., Horton, K.G., Loss, S.R., Cabrera-Cruz, S.A., Smolinsky, J.A., Marra, P.P., 2022. Using weather radar to help minimize wind energy impacts on nocturnally migrating birds. *Conserv. Lett.* 15 (4), e12887.
- de Felipe, M., Amat, J.A., Arroyo, J.L., Rodríguez, R., Díaz-Paniagua, C., 2024. Habitat changes at the local scale have major impacts on waterfowl populations across a migratory flyway. *Glob. Change Biol.* 30 (12), e17600.
- Delach, A., Nunes, L.A., Borowicz, A., Weber, T.C., 2024. Designated critical habitats for US imperiled species are not protected from climate and land-use change. *Geogr. Sustain.* 5 (3), 482–490.
- Drewitt, A.L., Langston, R.H.W., 2006. Assessing the impacts of wind farms on birds. *Ibis* 148, 29–42.
- Gallo-Cajiao, E., Morrison, T.H., Fuller, R.A., 2024. Agreements for conserving migratory shorebirds in the Asia-Pacific are better fit for addressing habitat loss than hunting. *Ambio* 53 (9), 1336–1354.
- Gardner, R.C., Finlayson, C., 2018. *Global Wetland Outlook: State of the World's Wetlands and Their Services to People*. Ramsar convention secretariat, pp. 2020–2025.
- Guan, J., 2023. The impact of onshore wind farms on ecological corridors in Ningbo, China. *Environ. Res. Commun.* 5 (1), 015006.
- Gurney, G.G., Adams, V.M., Alvarez-Romero, J.G., Claudet, J., 2023. Area-based conservation: taking stock and looking ahead. *One Earth* 6 (2), 98–104.
- Harris, P., Brunsdon, C., Charlton, M., 2011. Geographically weighted principal components analysis. *Int. J. Geogr. Inf. Sci.* 25 (10), 1717–1736.
- Hijmans, R.J., Barbosa, M., Ghosh, A., Mandel, A., Hijmans, M.R.J., 2024. Package 'geodata'. CRAN. <https://doi.org/10.32614/cran.package.geodata>.
- Hoffmann, S., Irl, S., Beierkuhnlein, C., 2019. Predicted climate shifts within terrestrial protected areas worldwide. *Nat. Commun.* 10, 4787.
- Huang, G., Hu, W., Du, J., Jia, Y., Zhou, Z., Lei, G., Saintilan, N., Wen, L., Wang, Y., 2025. Identification and scenario-based optimization of ecological corridor networks for waterbirds in typical coastal wetlands. *Ecol. Indic.* 171, 113147.
- IUCN, 2025. *The IUCN red list of threatened species. Version 2025-1*. <https://www.iucnredlist.org>. (Accessed 17 July 2025).
- Jiang, X., Mao, D., Zhen, J., Wang, J., van de Voorde, T., 2024. Exploring the conservation of historic Avian corridors under urbanization threats in China: a case study of egrets in the greater Bay area. *Sci. Total Environ.* 948, 174921.
- Keten, A., Eroglu, E., Kaya, S., Anderson, J.T., 2020. Bird diversity along a riparian corridor in a moderate urban landscape. *Ecol. Indic.* 118, 106751.
- Kii, M., Matsumoto, K., Sugita, S., 2024. Future scenarios of urban nighttime lights: a method for global cities and its application to urban expansion and carbon emission estimation. *Remote Sens.* 16 (6), 1018.
- Kujala, H., Moilanen, A., Araujo, M.B., Cabeza, M., 2013. Conservation planning with uncertain climate change projections. *PLoS One* 8 (2), e53315.
- Li, D., Li, B., Hou, X., Wang, X., Li, X., Zhang, Y., 2024. Habitat suitability assessment for Saunders's gull (*saundersilarus saundersi*) in the yellow river Delta, China. *Ecol. Inform.* 79, 102393.
- Liang, J., Wang, W., Cai, Q., Li, X., Zhu, Z., Zhai, Y., Li, X., Gao, X., Yi, Y., 2024. Prioritizing conservation efforts based on future habitat availability and accessibility under climate change. *Conserv. Biol.* 38 (3).
- Lin, F., Zhu, M., Dong, X., Ling, S., Luan, B., Pan, G., 2025. Revealing future effectiveness of protected areas for biodiversity conservation in the Guangdong-Hong Kong-Macao Greater Bay area. *Landsc. Urban Plann.* 255, 105260.
- Lin, G., Lan, S., Li, X., 2026. Identifying climate-resilient potential OECMs for migratory birds: a framework for future-oriented conservation planning. *Biol. Conserv.* 316, 111735.
- Lisovski, S., Hoyer, B., Conklin, J., Battley, P., Fuller, R., Gosbell, K., Klaassen, M., Lee, C., Murray, N., Bauer, S., 2024. Predicting Resilience of Migratory Birds to Environmental Change, 121. *Proceedings of the National Academy of Sciences*.
- Liu, F., Liu, J., Zhang, Y., Hong, S., Fu, W., Wang, M., Dong, J., 2024a. Construction of a cold island network for the urban heat island effect mitigation. *Sci. Total Environ.* 915, 169950.
- Liu, Q., Hang, T., Wu, Y., Song, Y., Tang, X., 2024b. Unveiling differences in biodiversity conservation efficiency across multi-level ecological networks under future climate change scenarios. *Ecol. Indic.* 169, 112933.
- Liu, R., Kong, H., Wang, Q., Li, Y., 2025. Identify priority protected areas for biodiversity conservation adapting to future climate and land cover changes. *Ecol. Indic.* 170, 113068.
- Liu, N., Ma, Z., 2024. Ecological restoration of coastal wetlands in China: current status and suggestions. *Biol. Conserv.* 291, 110513.
- Ma, Z., Hua, N., Peng, H., Choi, C., Battley, P.F., Zhou, Q., Chen, Y., Ma, Q., Jia, N., Xue, W., Bai, Q., Wu, W., Feng, X., Tang, C., 2013. Differentiating between stopover and staging sites: functions of the southern and northern yellow sea for long-distance migratory shorebirds. *J. Avian Biol.* 44 (5), 504–512.
- Ma, Z.J., Choi, C.Y., Gan, X.J., Li, J., Liu, Y., Melville, D.S., Mu, T., Piersma, T., Zhang, Z. W., 2023. Achievements, challenges, and recommendations for waterbird conservation in China's coastal wetlands. *Avian Res.* 14, 100123.
- Madsen, J., Boertmann, D., 2008. Animal behavioral adaptation to changing landscapes: spring-staging Geese habituate to wind farms. *Landsc. Ecol.* 23 (9), 1007–1011.
- Mantyka-Pringle, C.S., Visconti, P., Di Marco, M., Martin, T.G., Rondinini, C., Rhodes, J. R., 2015. Climate change modifies risk of global biodiversity loss due to land-cover change. *Biol. Conserv.* 187, 103–111.
- Marques, A.T., Batalha, H., Bernardino, J., 2021. Bird displacement by wind turbines: assessing current knowledge and recommendations for future studies. *Birds* 2 (4), 460–475.
- Marques, A.T., Batalha, H., Rodrigues, S., Costa, H., Ramos Pereira, M.J., Fonseca, C., Mascarenhas, M., Bernardino, J., 2014. Understanding bird collisions at wind farms: an updated review on the causes and possible mitigation strategies. *Biol. Conserv.* 179, 40–52.
- Marques, A.T., Santos, C.D., Hanssen, F., Munoz, A.-R., Onrubia, A., Wikelski, M., Moreira, F., Palmeirim, J.M., Silva, J.P., 2020. Wind turbines cause functional habitat loss for migratory soaring birds. *J. Anim. Ecol.* 89 (1), 93–103.
- Mehmood, K., Anees, S.A., Rehman, A., Pan, S.A., Tariq, A., Zubair, M., Liu, Q.J., Rabbi, F., Khan, K.A., Luo, M., 2024. Exploring spatiotemporal dynamics of NDVI and climate-driven responses in ecosystems: insights for sustainable management and climate resilience. *Ecol. Inform.* 80, 102532.
- Modica, G., Pratico, S., Laudari, L., Ledda, A., Di Fazio, S., De Montis, A., 2021. Implementation of multispecies ecological networks at the regional scale: analysis and multi-temporal assessment. *J. Environ. Manag.* 289, 112494.
- Morelli, T., Barrows, C., Ramirez, A., Cartwright, J., Ackerly, D., Eaves, T., Ebersole, J., Krawchuk, M., Letcher, B., Mahalovich, M., Meigs, G., Michalak, J., Miller, C., Quinones, R., Stralberg, D., Thorne, J., 2020. Climate-change refugia: biodiversity in the slow lane. *Front. Ecol. Environ.* 18, 228–234.
- Mossman, H.L., Panter, C.J., Dolman, P.M., 2015. Modelling biodiversity distribution in agricultural landscapes to support ecological network planning. *Landsc. Urban Plann.* 141, 59–67.
- Mott, R., Prowse, T.A.A., Jackson, M.V., Rogers, D.J., O'Connor, J.A., Brookes, J.D., Cassey, P., 2023. Measuring habitat quality for waterbirds: a review. *Ecol. Evol.* 13 (4), e09905.
- Mu, H., Guo, S., Li, X., Zhou, Y., Lu, Y., Du, X., Huang, J., Ma, C., Zhang, X., Xia, Z., Fang, H., Du, P., 2024. Quantifying landscape connectivity gaps between protected area and natural habitat. *J. Clean. Prod.* 437, 140729.
- Muscarella, R., Galante, P.J., Soley-Guardia, M., Boria, R.A., Kass, J.M., Uriarte, M., Anderson, R.P., 2014. ENM eval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for maxent ecological niche models. *Methods Ecol. Evol.* 5 (11), 1198–1205.
- Nazarnia, H., Nazarnia, M., Sarmasti, H., Wills, W.O., 2020. A systematic review of civil and environmental infrastructures for coastal adaptation to sea level rise. *Civil Engineering Journal-Tehran* 6 (7), 1375–1399.
- Patankar, S., Jambhekar, R., Suryawanshi, K.R., Nagendra, H., 2021. Which traits influence bird survival in the city? A review. *Land* 10 (2), 92.
- Peng, H.-B., Zhu, Z., Choi, C.-Y., Mu, T., Huang, Y., Li, J., Lei, W., Bouma, T., Melville, D., Zhang, Z.-W., Ma, Z., Lei, G., Yang, Z., Piersma, T., 2025. China's intertidal mariculture as an unexpected lifeline sustaining the world's most threatened shorebird flyway. *Nat. Commun.* 16.
- Ross-Smith, V.H., Thaxter, C.B., Masden, E.A., Shamoun-Baranes, J., Burton, N.H.K., Wright, L.J., Rehfish, M.M., Johnston, A., 2016. Modelling flight heights of lesser black-backed gulls and great skuas from GPS: a Bayesian approach. *J. Appl. Ecol.* 53 (6), 1676–1685.
- Santini, L., Saura, S., Rondinini, C., 2016. Connectivity of the global network of protected areas. *Divers. Distrib.* 22 (2), 199–211.
- 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.
- Sillero, N., 2011. What does ecological modelling model? A proposed classification of ecological niche models based on their underlying methods. *Ecol. Model.* 222 (8), 1343–1346.
- Spiliopoulou, K., Brooks, T.M., Dimitrakopoulos, P.G., Oikonomou, A., Karavatsou, F., Stoumboudi, M.T., Triantis, K.A., 2023. Protected areas and the ranges of threatened species: towards the EU biodiversity strategy 2030. *Biol. Conserv.* 284, 110166.
- Stralberg, D., Carroll, C., Nielsen, S.E., 2020. Toward a climate-informed North American protected areas network: incorporating climate-change refugia and corridors in conservation planning. *Conserv. Lett.* 13 (4), e12712.
- Su, J., Kong, F., Yin, H., Meadows, M.E., Chen, L., He, H.S., Sun, H., Li, Z., Zhou, K., Chen, B., 2025. Essential contribution of habitats in non-protected areas to climate-driven species migration in China. *Geogr. Sustain.* 6 (1), 100203.
- Teng, H.F., Chen, S.C., Hu, B.F., Shi, Z., 2023. Future changes and driving factors of global peak vegetation growth based on CMIP6 simulations. *Ecol. Inform.* 75, 102031.
- Tolvanen, A., Routavaara, H., Jokikokko, M., Rana, P., 2023. How far are birds, Bats, and terrestrial mammals displaced from onshore wind power development? - a systematic review. *Biol. Conserv.* 288, 110382.
- Wang, X.D., Chen, Y., Melville, D.S., Choi, C.Y., Tan, K., Liu, J.J., Li, J., Zhang, S.D., Cao, L., Ma, Z.J., 2022. Impacts of habitat loss on migratory shorebird populations and communities at stopover sites in the yellow sea. *Biol. Conserv.* 269, 109547.
- Wang, Y.Y., Chao, B.X., Dong, P., Zhang, D.A., Yu, W.W., Hu, W.J., Ma, Z.Y., Chen, G.C., Liu, Z.H., Chen, B., 2021. Simulating spatial change of mangrove habitat under the impact of coastal land use: coupling MaxEnt and Dyna-CLUE models. *Sci. Total Environ.* 788, 147914.
- Wauchope, H.S., Jones, J.P.G., Geldmann, J., Simmons, B.I., Amano, T., Blanco, D.E., Fuller, R.A., Johnston, A., Langendoen, T., Mundkur, T., Nagy, S., Sutherland, W.J., 2022. Protected areas have a mixed impact on waterbirds, but management helps. *Nature* 605 (7908), 103.
- Wei, X.L., Ji, Y.R., Jia, R., Li, Q.L., Ma, C.X., Song, X.K., Cheng, F.W., Yin, H.Q., Xu, F.Y., Yu, H.Y., Sun, G., Wang, X.L., Li, D.Q., Zhang, G.G., 2024. Projected expansion in

- two influenza-susceptible birds' distribution under climate and land-cover changes on the Qinghai-Tibetan Plateau. *Glob. Ecol. Conserv.* 56, e03305.
- Wikramanayake, E., Or, C., Costa, F., Wen, X., Cheung, F., Shapiro, A., 2020. A climate adaptation strategy for Mai Po inner deep Bay Ramsar site: steppingstone to climate proofing the East Asian-Australasian flyway. *PLoS One* 15 (10), e0239945.
- Xin, Y., Lu, N., Jiang, H., Liu, Y., Yao, L., 2021. Performance of ERA5 reanalysis precipitation products in the Guangdong-Hong Kong-Macao greater Bay area, China. *J. Hydrol.* 602, 126791.
- Xu, D., Peng, J., Liu, M., Jiang, H., Tang, H., Dong, J., Meersmans, J., 2024a. Bridging climate refuges for climate change adaptation: a spatio-temporal connectivity network approach. *Geogr. Sustain.* <https://doi.org/10.1016/j.geosus.2024.08.012>.
- Xu, W., Yang, H., Chen, Z., Shi, R., Liu, Y., Chen, J., 2024b. Enhancing bird habitat networks in metropolitan areas: resilience assessment and improvement strategies - a case study from Shanghai. *Sci. Total Environ.* 954, 176316.
- Yang, C., Li, Q., Hu, Z., Chen, J., Shi, T., Ding, K., Wu, G., 2019. Spatiotemporal evolution of urban agglomerations in four major bay areas of US, China and Japan from 1987 to 2017: evidence from remote sensing images. *Sci. Total Environ.* 671, 232–247.
- Yang, H., Xu, W., Chen, Z., Xie, X., Yu, J., Lei, X., Guo, S., Ding, Z., 2024. Ecological network construction for bird communities in high-density urban areas: a perspective of integrated approaches. *Ecol. Indic.* 158, 111592.
- Yang, X., Liu, W., Li, S., Ma, Z., Chen, C., Gu, W., Qu, M., Zhang, C., Ding, Z., Xu, Y., 2022. Restoration of urban waterbird diversity: a case study of the construction of a waterbird ecological corridor in the Guangdong-Hong Kong-Macao greater Bay area, southern China. *Glob. Ecol. Conserv.* 39, e02277.
- Ye, Y., Chen, C., Yu, C., Sun, C., Geng, S., 2025. Identifying stepping-stones within small wetlands in highly urbanized areas and under network construction: a case study of the Guangdong-Hong Kong-Macao greater Bay Area, China. *Ecol. Indic.* 176, 113622.
- Yoon, H.J., Joo, E.J., Ha, D.S., Nam, H.K., Yoon, J., 2018. Does nest predation influence colony movements of saunders's gulls (*Saundersilarus Saundersi*) in a reclaimed land area? *Zool. Sci.* 35 (5), 389–395.
- Zhang, M., Hong, Y., Zou, F., Zhang, Q., Fan, H., Chan, S., Cheong, K.-t., Leong, K.-F., 2019. Response of shorebird habitat selection to coastal reclamation and urbanization in an extensively developed Delta: a case study in Macao, China. *Ocean Coast Manag.* 179, 104871.
- Zhang, X., Chen, Y., Xu, Y., Yue, W., Tang, C., 2023. Does regional cooperation constrain urban sprawl? Evidence from the Guangdong-Hong Kong-Macao greater Bay area. *Landsc. Urban Plann.* 235, 104742.
- Zhao, Y., Qian, W., Liu, X., Wu, C., 2024. Assessing and optimizing the effectiveness of protected areas along China's coastal region: a social-ecological protected area network study. *J. Environ. Manag.* 349, 119338.
- Zockler, C., Beresford, A.E., Bunting, G., Chowdhury, S.U., Clark, N.A., Fu, V.W.K., Hla, T.H., Morozov, V.V., Syroechkovskiy, E.E., Kashiwagi, M., Lappo, E.G., Tong, M., Trai Le, L., Yu, Y.-T., Huettmann, F., Akasofu, H.K., Tomida, H., Buchanan, G.M., 2016. The winter distribution of the spoon-billed sandpiper *calidris pygmaea*. *Bird. Conserv. Int.* 26 (4), 476–489.