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Exploring the driving factors of bird diversity in mangrove natural protected areas in Guangdong Province, China

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Introduction: Under the impacts of high intensity human activities, mangrove natural protected areas are pivotal strategies for biodiversity conservation and play a significant role in preserving bird diversity. Mangrove natural protected areas in Guangdong Province, China, lie along the migratory path of the East Asian–Australasian Flyway, serving as breeding, feeding, and resting grounds for birds. Variations in bird responses to environmental factors are significant.

Methods: To comprehensively understand these variances, redundancy analysis was employed, focusing on bird diversity surveys conducted from March 2022 to February 2023 in natural protected areas of Guangdong to examine how driving factors such as mangrove habitat landscape, community structure, water quality, and soil sedimentation affected the diversity of avian species.

Results: The findings were as follows: (1) A total of 193 bird species spanning 17 orders and 53 families were documented, including 74 songbirds, 60 wading birds, 27 swimming birds, 17 climbing birds, 10 raptors, and 5 terrestrial birds. (2) Regarding the impact of simple effects on all bird species, aquaculture pond area, mangrove extent, and mudflat area emerged as significant factors driving bird diversity, with explanatory rates of 31.0%, 28.9%, and 20.3%, respectively. Notably, the aquaculture pond area was the main driver of bird diversity, with an explanatory rate of 31.0%. (3) Mangrove extent has emerged as a pivotal factor shaping the songbird diversity, climbing birds, raptors, and terrestrial birds, whereas the aquaculture pond area was pivotal for wading birds, swimming birds, and others.

Discussion: To enhance mangrove bird diversity protection, management agencies overseeing natural mangrove protected areas should adopt science-based approaches when managing mangrove, mudflats, and aquaculture pond areas in mangrove forest protection and restoration plans. This would prevent

extensive mangrove planting, which encroaches on non-mangrove habitats. Additionally, the scientific management of aquaculture ponds should accommodate diverse bird habitats through measures, such as water level adjustments.

KEYWORDS

mangrove, natural protected areas, bird, habitat, diversity, factor

1 Introduction

In recent decades, global bird diversity has declined, primarily because of rapid socioeconomic development (Yasué, 2006; Ma et al., 2014; Hamza et al., 2015; Wei et al., 2017; Jackson et al., 2021). This decline is particularly pronounced in the coastal regions of China. Despite its location in the migratory route of the East Asian-Australasian Flyway and its significant role in global migratory bird protection, China has experienced a noteworthy decline in the diversity of nearly 19% of waterbirds due to the degradation of coastal habitats resulting from human disturbance (Ma et al., 2014). Notably, the decline in bird diversity in the mangrove ecosystems of South China is particularly severe.

As integral components of coastal wetlands, mangroves serve multiple functions, including resistance to natural disaster risk (Menéndez et al., 2018), acting as a carbon sink (Gu et al., 2022), maintaining high biodiversity (Mancini et al., 2018; Jackson et al., 2021; Yang et al., 2021), and even becoming a refuge for some flagship species (Thompson and Stefanie, 2019). Owing to the fragility of mangrove ecosystems, restoration of their original state is challenging (Ren, 2009). Consequently, the Chinese government has designated over 90% of mangroves into the system of natural protected areas through constructing natural protected areas (Li et al., 2013). Simultaneously, expanding mangrove planting within these areas facilitates rapid ecosystem restoration and structural reshaping (Leung, 2015), thereby laying the groundwork for improving bird habitat quality and restoring biodiversity. Guangdong Province, which has the largest mangrove distribution in China with an area of 12092.95 ha, accounting for 41.9% of China's mangroves (excluding Hong Kong, Macao, and Taiwan), harbors over 50% of its mangroves within protected areas. This region serves as a crucial stopover and provisioning site for migratory birds and is important for the conservation of both Chinese and global avian migrants.

Previous studies have demonstrated that mangrove bird diversity is influenced by a range of complex factors, including landscape features (Yang et al., 2021, 2022; Ahmed et al., 2023; Wanjiru et al., 2023), mangrove community structure (Etezadifar and Ahmad, 2013; Leung and Nora, 2013; Mancini et al., 2018), water environment (Caussey, 2009), and soil sedimentary environment (Weinstein and Daniel, 2002; Cannicci et al., 2008). Optimizing the ratio of mangroves to mudflat areas through scientific management can enhance bird

diversity (Yang et al., 2021). Mangroves with singular habitats may provide limited microhabitats and specialized ecological niches, resulting in low bird species richness and simplified structures (Jayasilan et al., 2015). Additionally, the relatively small average height of mangrove canopies may affect egret canopy utilization (Mancini et al., 2018). Furthermore, water (Caussey, 2009) and soil conditions (Weinstein and Daniel, 2002; Cannicci et al., 2008) can affect bird diversity by affecting benthic organism diversity. These studies primarily examined the effects of individual factors on bird diversity; however, complex interactions among these factors exist within a nonlinear system. Different bird species exhibit distinct responses to shared driving factors (Hamza et al., 2015), highlighting the need for researchers to comprehensively understand these variations and identify key drivers of bird diversity to inform future mangrove bird conservation and habitat restoration efforts.

Therefore, based on the study of bird diversity in protected mangrove areas in Guangdong Province, we utilized the redundancy analysis (RA) analysis method to explore how various factors, such as mangrove habitat landscape, mangrove community structure, water environment, and soil sedimentary environment, affect different types of bird diversity. By analyzing various bird responses to these factors, we identified the key drivers of bird diversity and enhanced future conservation efforts.

2 Regional overview and methods

2.1 Regional overview

China has experienced mangrove destruction, protection, and restoration. Despite efforts to restore mangrove ecosystem functions by planting native species in natural protected areas, over 80% of restored mangroves remain as degraded secondary forests (Sui and Zhang, 2001). Additionally, species such as *Sonneratia apetala* were selected as the main species for recovery. As a result, some natural protection areas still retain large areas of *Sonneratia apetala* (Chen et al., 2017).

Guangdong Province, situated in the southernmost region of mainland China, has a mainland coastline spanning 4114.3 km and an island coastline spanning 1649.5 km. Mangrove species prevalent in Guangdong include *Kandelia obovata*, *Aegiceras corniculatum*, *Avicennia marina*, *Bruguiera gymnorhiza*, *Rhizophora stylosa*,

Acanthus ilicifolius, *Acrostichum aureum*, and *Sonneratia apetala*. These mangrove resources are distributed across 46 counties (cities and districts) in 13 prefecture-level cities along the coast, totaling 12092.95 ha, representing 41.9% of China’s mangrove area (excluding Hong Kong, Macao, and Taiwan). Notably, 50.20% of these mangroves are situated within 20 natural protected areas, including the Zhanjiang Mangrove National Nature Reserve, Zhuhai Qi’ao-Dangan Island Provincial Nature Reserve, and Jiangmen Taishan Zhenhai Mangrove National Wetland Park (Table 1 and Figure 1). All 20 naturally protected areas were included in this study. In some of these protected areas, abandoned aquaculture ponds are not used for economic farming. Instead, managers utilize tides to facilitate the exchange of aquatic resources inside and outside abandoned aquaculture ponds, providing food for birds inhabiting mangrove forests. These aquaculture ponds are a crucial part of the mangrove ecosystems. Additionally, some of these protected areas are connected to land rich in grasslands and shrublands. For example, Zhanjiang Jiulongshan Mangrove the National Wetland Park is connected to such land, and Galliformes inhabit areas between mangroves and grassland, with mangroves serving as a supplemental food source.

2.2 Methods

2.2.1 Determine of survey line transects, survey quadrats, and sampling points

2.2.1.1 Bird survey line transects

In ArcGIS 10.2, the coastal area of Guangdong Province was partitioned into 10 × 10 km grids using the kilometer grid method (Yang et al., 2021). These grids were overlaid with the boundary ranges

TABLE 1 Overview of mangrove ecosystems in natural protected areas, Guangdong Province.

Number	Name of the natural protected areas	Mangrove species
1	Guangzhou Nansha Wetland Park	<i>Sonneratia apetala</i> , <i>Bruguiera gymnorhiza</i> , <i>Pongamia pinnata</i> , <i>Kandelia obovata</i>
2	Shenzhen Futian-Neilingding National Nature Reserve	<i>Kandelia obovata</i> , <i>Aegiceras corniculatum</i> , <i>Avicennia marina</i>
3	Shenzhen Dapeng Peninsula Municipal Nature Reserve	<i>Sonneratia apetala</i> , <i>Kandelia obovata</i> , <i>Bruguiera gymnorhiza</i>
4	Shenzhen Overseas Chinese Town National Wetland Park	<i>Heritiera littoralis</i> , <i>Avicennia marina</i> , <i>Kandelia obovata</i> , <i>Aegiceras corniculatum</i>
5	Zhuhai Qiao-Dangan Island Provincial Nature Reserve	<i>Sonneratia apetala</i> , <i>Avicennia marina</i> , <i>Kandelia obovata</i> , <i>Bruguiera gymnorhiza</i> , <i>Rhizophora stylosa</i> , <i>Aegiceras corniculatum</i>

(Continued)

TABLE 1 Continued

Number	Name of the natural protected areas	Mangrove species
6	Zhuhai Hengqin National Wetland Park	<i>Avicennia marina</i> , <i>Rhizophora stylosa</i> , <i>Sonneratia apetala</i> , <i>Kandelia obovata</i> , <i>Bruguiera gymnorhiza</i>
7	Zhongshan Cuiheng National Wetland Park	<i>Sonneratia apetala</i>
8	Huizhou Huidong Mangrove Municipal Nature Reserve	<i>Sonneratia apetala</i> , <i>Acanthus ilicifolius</i> , <i>Bruguiera gymnorhiza</i> , <i>Aegiceras corniculatum</i> , <i>Kandelia obovata</i> , <i>Pongamia pinnata</i> , <i>Heritiera littoralis</i> , <i>Talipariti tiliaceum</i>
9	Huidong Yanzhou Island Mangrove County Wetland Park	<i>Kandelia obovata</i>
10	Huizhou Daya Bay Mangrove Urban Wetland Park	<i>Sonneratia apetala</i>
11	Jiangmen Taishan Zhenhai Mangrove National Wetland Park	<i>Kandelia obovata</i> , <i>Sonneratia apetala</i>
12	Yangjiang Hailingdao Mangrove National Wetland Park	<i>Kandelia obovata</i> , <i>Aegiceras corniculatum</i> , <i>Avicennia marina</i>
13	Yangxi Haoguang Mangrove County Nature Reserve	<i>Kandelia obovata</i> , <i>Aegiceras corniculatum</i>
14	Yangdong Shouchanghe Mangrove National Wetland Park	<i>Avicennia marina</i> , <i>Acanthus ilicifolius</i> , <i>Aegiceras corniculatum</i> , <i>Kandelia obovata</i> , <i>Acrostichum aureum</i> , <i>Sonneratia apetala</i>
15	Maoming Maogang Mangrove County Nature Reserve	<i>Laguncularia racemosa</i> , <i>Sonneratia apetala</i> , <i>Avicennia marina</i>
16	Maoming Dianbai Mangrove County Nature Reserve	<i>Laguncularia racemosa</i> , <i>Avicennia marina</i> , <i>Kandelia obovata</i> , <i>Aegiceras corniculatum</i> , <i>Sonneratia apetala</i>
17	Zhanjiang Mangrove National Nature Reserve	<i>Avicennia marina</i> , <i>Rhizophora stylosa</i> , <i>Bruguiera gymnorhiza</i> , <i>Aegiceras corniculatum</i> , <i>Kandelia obovata</i> , <i>Acanthus ilicifolius</i> , <i>Sonneratia apetala</i>
18	Zhanjiang Jiulongshan Mangrove National Wetland Park	<i>Avicennia marina</i> , <i>Rhizophora stylosa</i> , <i>Sonneratia apetala</i>
19	Shantou Wetland Municipal Nature Reserve	<i>Sonneratia apetala</i> , <i>Aegiceras corniculatum</i>
20	Shanwei Haifeng Bird Provincial Nature Reserve (Lian An Wei Area)	<i>Sonneratia apetala</i> , <i>Laguncularia racemosa</i> , <i>Avicennia marina</i> , <i>Aegiceras corniculatum</i> , <i>Kandelia obovata</i>

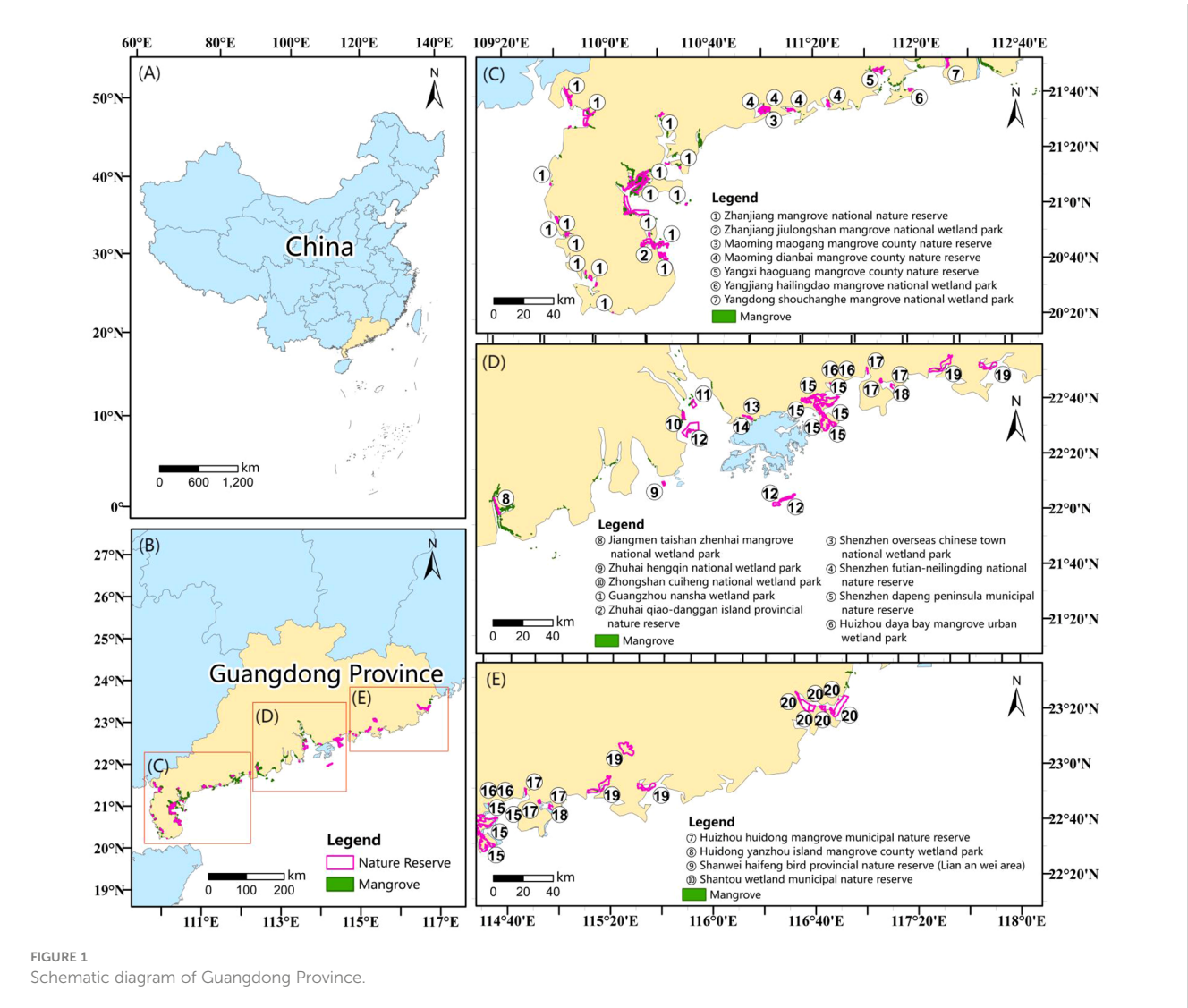


FIGURE 1
Schematic diagram of Guangdong Province.

of 20 natural protected areas. If an entire protected area fell within a grid, a 6 km line transect traversing the mangrove ecosystem was established within that grid. A total of 41 transect lines were included in the survey. Specifically, 21 line transects were established in the Zhanjiang Mangrove National Nature Reserve, 2 in the Jiangmen Taishan Zhenhaiwan Mangrove National Wetland Park, and 1 in each of the remaining protected areas.

2.2.1.2 Mangrove community survey quadrats

Mangrove coverage within the specified grids was assessed using ArcGIS 10.2, with measurements performed for the length of coverage in each grid. Within each grid, 5 quadrats, measuring 20 m × 20 m, were selected at regular intervals. In total 205 survey samples were collected.

2.2.1.3 Sampling points for water and soil environmental factors sampling points

5 collection points for water and soil environmental factors were selected from the aforementioned quadrats. In total, 205 survey samples were collected.

2.2.2 Survey methods

2.2.2.1 Bird diversity

Bird surveys were conducted during both the breeding period (March to May 2022) and wintering period (October to December 2022), with two surveys completed during each period. All surveys were performed by the same staff members to ensure the accuracy of observations. Each survey sample line was 6 km long, and the survey was conducted on foot. Surveys were conducted either in the morning (7:00–11:30) or afternoon (3:00–6:30), each lasting up to 3 h, with low tide identified as the optimal time for assessing bird diversity (Jimenez et al., 2015; Fonseca et al., 2017; Horn et al., 2020). Tide tables from the official website of the China Marine Service Network (Ocean.cnss.com.cn) were checked to determine the low-tide timings for survey scheduling. Field survey equipment included TSN841 20-60x monocular telescopes and 1000 m telephoto lenses for recording assistance. In this study, the species names and individual numbers of birds were collected. Due to the presence of 20 protected natural areas along the migratory route of the East Asian-Australasian Flyway, these areas play a significant role in global migratory bird protection. This is particularly important for special birds, such as migrating

geese, ducks, and swifts, which can use mangroves for rest or as a food source. Field personnel comprised experienced researchers with expertise in bird observation. Bird identification references included *A Field Guide to the Birds of China* (MacKinnon and Phillipps, 2000). Resident type references include *A Checklist on the Classification and Distribution of the Birds in China*(Fourth Edition) (Zheng, 2023).

The surveyed birds were categorized into six ecological types based on their habits and morphological characteristics, namely songbirds, terrestrial birds, climbing birds, swimming birds, wading birds, and raptors (Table 2). Songbirds, primarily passerine birds,

are adept at singing via the syrinx control. Terrestrial birds have relatively short beaks, typically living in flocks, and can be either terrestrial or arboreal, they primarily move on the ground in search of food, and include species, such as Galliformes. Climbing birds, such as Caprimulgiformes, Apodiformes, Piciformes and Coraciiformes, have two toes pointing forward and two toes pointing backward, which facilitates tree climbing. Swimming birds, including Anseriformes, Anseriformes, Podicipediformes, and Lariformes, have webbed toes and wide or sharp beaks, that enable them to excel at swimming, diving, and foraging in water,

TABLE 2 Land-use in natural protected areas.

Name of the natural protected areas	Total area (ha)	Mangrove area (%)	Mudflat (%)	Aquaculture pond area (%)	Water body area (%)	Forests, shrubland, and grasslands that grow on land (%)
Guangzhou Nansha Wetland Park	992.27	8.06	14.95	32.63	40.80	3.57
Shenzhen Futian-Neilingding National Nature Reserve	387.42	29.60	25.48	13.11	20.79	11.02
Shenzhen Dapeng Peninsula Municipal Nature Reserve	14633.87	0.05	0.10	0.12	2.16	97.57
Shenzhen Overseas Chinese Town National Wetland Park	68.15	6.05	21.03	0.00	28.81	44.12
Zhuhai Qi'ao-Danggan Island Provincial Nature Reserve	6777.15	7.28	37.33	0.18	28.68	26.53
Zhuhai Hengqin National Wetland Park	314.36	0.32	37.98	30.40	10.63	20.67
Zhongshan Cuiheng National Wetland Park	629.34	9.70	0.55	4.45	55.01	30.29
Huizhou Huidong Mangrove Municipal Nature Reserve	574.98	11.83	8.61	26.82	49.25	3.50
Huidong Yanzhou Island Mangrove County Wetland Park	61.88	17.16	18.44	0.00	63.64	0.76
Huizhou Daya Bay Mangrove Urban Wetland Park	11.19	89.28	5.31	0.00	5.31	0.11
Jiangmen Taishan Zhenhai Mangrove National Wetland Park	560.32	26.40	16.39	10.39	14.12	32.70
Yangjiang Hailingdao Mangrove National Wetland Park	189.8	16.98	48.75	16.05	18.17	0.05
Yangxi Haoguang Mangrove County Nature Reserve	1163.2	17.40	33.86	22.15	12.91	13.68
Yangdong Shouchanghe Mangrove National Wetland Park	406.85	26.56	4.39	0.00	49.67	19.38
Maoming Maogang Mangrove County Nature Reserve	1945.18	5.92	34.13	3.28	52.34	4.33
Maoming Dianbai Mangrove County Nature Reserve	799.33	22.80	20.81	8.13	20.81	27.44
Zhanjiang Mangrove National Nature Reserve	20518.2	20.67	24.39	31.21	23.50	0.23
Zhanjiang Jiulongshan Mangrove National Wetland Park	1508.44	7.92	28.49	17.69	29.94	15.95
Shantou Wetland Municipal Nature Reserve	10324	0.20	33.57	7.51	50.09	8.63
Shanwei Haifeng Bird Provincial Nature Reserve	11535	0.45	15.24	28.55	8.21	47.55

although most are not adept at walking on land. Wading birds, adapted to live in shallow waters or along shores, have long beaks, necks, and legs, making them suitable for wading but not for swimming, this group includes Ciconiiformes, Gruiformes, and Charadriiformes. Raptors, including Accipitriformes and Falconiformes, have powerful hooked beaks, large wings, strong feet, and sharp talons, they prey on other birds, mice, rabbits, and snakes, or feed on carrion.

2.2.2.2 Mangrove plant species and community

Mangroves are crucial ecosystems for bird reproduction, roosting, and feeding, and bird habitat utilization is closely linked to vegetation structure. Investigating the impact of mangrove communities on bird diversity involves assessing crown width, crown height, tree height, diameter at breast height (ground diameter), and mangrove plant species composition (Etezdifar and Ahmad, 2013; Leung and Nora, 2013; Mancini et al., 2018). Therefore, measurements of all mangrove plants were conducted within the survey quadrats during March-May and October-December 2022, and their average values were calculated.

2.2.2.3 Water and soil environmental factors

The physical and chemical conditions of mangrove water and soil environments not only indicate the ability of mangroves to accumulate and purify harmful substances, but also affect the biodiversity of the biological community it supports (Weinstein and Daniel, 2002; Cannicci et al., 2008). Previous studies have typically investigated parameters such as pH, water temperature, salinity, dissolved oxygen, soil salinity, chemical oxygen demand, nitrite, nitrate, ammonia, and suspended solids in aquatic environments (Caussy, 2009), as well as organic matter, sulfide, inorganic phosphorus, and reactive silicate in sedimentary environments (Weinstein and Daniel, 2002; Cannicci et al., 2008) to assess their effects on biodiversity. Hence, water quality and soil sediment environmental data were collected during the wet season (June–August) and dry season (November–December) of 2022, and the average values of these factors within each protected area were computed.

Water environmental factor detection method: At high water levels, water samples (1 L) were collected in brown glass bottles at each sampling point. A portable water quality detector (COD Ammonia Nitrogen Total Phosphorus Total Nitrogen analyzer) was used on-site to test pH, water temperature, salinity, dissolved oxygen, soil salinity, chemical oxygen demand, nitrite, nitrate, ammonia, suspended matter, and other factors. Data were recorded accordingly.

Sedimentary environmental factor detection method: Samples were collected at low tide, and surface sediment samples (10 cm) were taken from each sampling point. These samples were then brought back to the laboratory for the analysis of sedimentary environmental factors. The following methods were employed in the analysis of various components: thermal conductivity for organic matter, spectrophotometry for active silicate, the iodine method for sulfide, and digestion-molybdenum-antimony resistance spectrophotometry for inorganic phosphorus.

2.2.2.4 Mangrove habitat area

Within mangrove ecosystems, factors such as mangrove area, mudflat extent, aquaculture pond coverage, and open water areas (excluding aquaculture) play significant roles in shaping bird diversity. Remote sensing imagery for 2022 was acquired from the Data Center for Resources and Environmental Sciences, at the Chinese Academy of Sciences (RESDC, <http://www.resdc.cn>). Geometric and radiometric corrections were performed using the ENVI 5.3 software. The processed data underwent on-site verification, with mangroves, mudflats, aquaculture ponds, and open water areas quantified within each natural protection area.

2.2.3 Data processing

2.2.3.1 Correlation analysis of environmental factors

The Kolmogorov-Smirnov normal distribution test was performed for all factors, with a significance level of 0.05. The results showed that mangrove area, aquaculture pond area, open water area, sulfide, inorganic phosphorus, and other factors did not follow a normal distribution, whereas the remaining factors did. Pearson's correlation analysis was used to examine correlations between environmental factors with a normal distribution, and rank correlation analysis was employed for those with a non-normal distribution. All analyses were conducted using SPSS 16.0 software. The analysis revealed that 5 environmental factors, including crown value, diameter at breast height (ground diameter), tree height, nitrate, and soil salinity, were correlated with other factors and were therefore excluded from further analysis.

2.2.3.2 Data standardization

Given the diverse types and dimensions of environmental factors, standardizing initial data is imperative (Cheng et al., 2021). The range method was employed to standardize the quantitative indices. A higher positive index value corresponds to a greater function, whereas a lower negative index value corresponds to a smaller function. Equations 1 and 2 can be used to standardize positive and negative indicators, respectively.

$$Z_{ij} = \frac{X_{ij} - X_{jmin}}{X_{jmax} - X_{jmin}} \quad (1)$$

$$Z_{ij} = \frac{X_{jmax} - X_{ij}}{X_{jmax} - X_{jmin}} \quad (2)$$

where Z_{ij} is the standardized value of the environmental factor, and its value ranges from 0 to 1; X_{ij} is the j value of the i indicator; X_{jmin} is the minimum value of the i indicator; and X_{jmax} is the maximum value of the i indicator.

2.2.3.3 Redundancy analysis

To identify the primary drivers of bird diversity, RA was employed to assess the correlation between birds and their drivers, a widely used method in environmental studies (Zhang et al., 2016; Wang et al., 2021). First, detrended correspondence analysis (DCA) determined the linearity or unimodal response model of the analysis. The standardized sum-transformed species population square matrix served as the response variable. For the explanatory variables, we

adopted a log10 transformation [$\log_{10}(x + 1)$]. Given that the first four DCA axes exhibited maximum gradient lengths of less than 2, RA was selected for further analysis of the driving factors and bird diversity. To incorporate more factors into the analysis, a forward selection procedure identified variables with significant effects ($P < 0.1$), excluding those deemed insignificant ($P > 0.1$), because in very significant cases ($P < 0.05$), only a few factors were included in the analysis. The significance of each variable was evaluated using the RA and a Monte Carlo permutation test with 999 permutations. DCA and RA analyses were predominantly conducted using CANOCO version 5.0.

3 Results

3.1 Land-use type

As shown in Table 2, the land-use types of each nature reserve were diverse, and the mangrove ecosystem was coupled with the terrestrial ecosystem. This coupling provides complex habitat requirements for various bird species.

3.2 Bird diversity

A comprehensive survey recorded 193 bird species, belonging to 17 orders and 53 families. Among these, there were 74 songbirds, 60 wading birds, 27 swimming birds, 17 climbing birds, 10 raptors, and 5 terrestrial birds (Table 3).

Among the recorded species, 28 were listed in “China’s National Key Protected Species List”, namely Eastern white pelican (*Pelecanus onocrotalus*), Saunders’s gull (*Larus saundersi*), Spotted greenshank (*Tringa guttifer*), and Eurasian spoonbill (*Platalea leucorodia*). Additionally, 78 species were included in the “Agreement Between the Government of the People’s Republic of China and the Government of Japan for the Protection of Migratory Birds and Habitat Environment” (1981), including Bean goose (*Anser fabalis*), Fork-tailed swift (*Apus pacificus*), Common moorhen (*Gallinula chloropus*), Black-headed gull (*Larus ridibundus*), and Besra (*Accipiter virgatus*). Furthermore, 34 recorded species were listed in the “Agreement Between the Government of the People’s Republic of China and the Government of Australia for the Protection of Migratory Birds and Their Habitat Environment” (1986). This indicated the significant role played by the coastal areas of Guangdong Province in safeguarding the biodiversity of birds in China and globally.

3.3 Resident types of birds

The 193 species of birds consisted of 93 species of winter visitors (49.18%), 15 species of summer visitors (7.77%), 70 species of residents (36.27%), 13 species of passage migrants (6.74%), and 2 species of vagrant visitors (1.04%). Mangrove ecosystems within protected areas of Guangdong Province are pivotal for preserving the diversity of migratory bird species.

3.4 Characteristics of driving factors

The basic conditions for each driving factor are listed in Table 4, where each factor shows its minimum, maximum, and average values. Data were collected from all transects.

3.5 Bird diversity and RA analysis of environmental factors

This study examined the effects of environmental factors and human disturbances on various bird categories, including birds, songbirds, wading birds, swimming birds, climbing birds, raptors, and terrestrial birds, using the RA method. The sorting results of RA are presented in Table 5.

The cumulative explanation of the variance in the species-environment relationship for all typical axes for all birds was approximately 83.10%. Significance of the Monte Carlo permutation tests for all positive axes was observed ($p < 0.05$). The eigenvalues of the first two canonical axes significantly exceeded those of the remaining axes, signifying their principal explanatory roles. These two axes accounted for approximately 49.13% and 17.51% of the variation, respectively, demonstrating their efficacy in elucidating relationships between species and environmental variables.

Similarly, for songbirds, wading birds, swimming birds, climbing birds, raptors, and terrestrial birds, the cumulative explanation of the variance in the species-environment relationship across all typical axes exceeded 90%. Monte Carlo permutation tests indicated significance ($p < 0.05$), and the first two typical axes effectively elucidated the relationship between species and environmental variables.

3.6 Relationships between birds and habitat characteristics

In Figure 2, the red arrow represents the environmental factor, and the blue line indicates the species factor. The length of the arrow indicates the strength of the correlation between the bird diversity and environmental factors. The angle formed between the arrow and ranking axis reflects the magnitude of the correlation between the environmental factor and ranking axis. A small angle indicates a strong correlation. Furthermore, the quadrant in which the arrow is located indicates whether the correlation between the azimuth environmental factor and ranking axis is positive or negative.

As shown in Figure 2A and Table 6, for all birds, the aquaculture pond, mangrove, and mudflat areas were identified as significant drivers of bird diversity, with interpretation rates of 31.0%, 28.9%, and 20.3%, respectively, in terms of simple effects. Regarding conditional effects, aquaculture pond area emerged as the main factor, explaining 31.0% of the bird diversity. Hence, the area of aquaculture ponds significantly affected the bird diversity.

Various bird species exhibit distinct sensitivities to identical driving factors.

TABLE 3 Composition of different types of birds in natural protected areas, Guangdong Province.

Guild	Species name
Songbird	Ashy minivet (<i>Pericrocotus divaricatus</i>), Black drongo (<i>Dicrurus macrocerus</i>), Spangled drongo (<i>Dicrurus hottentottus</i>), Brown shrike (<i>Lanius cristatus</i>), Long-tailed shrike (<i>Lanius Schach</i>), Grey-backed shrike (<i>Lanius tephronotus</i>), Eurasian jay (<i>Garrulus glandarius</i>), Azure-winged magpie (<i>Cyanopica cyanus</i>), Red-billed blue magpie (<i>Urocissa erythrorhyncha</i>), Grey treepie (<i>Dendrocitta formosae</i>), Black-billed magpie (<i>Pica pica</i>), Collared crow (<i>Corvus pectoralis</i>), Large-billed crow (<i>Corvus macrorhynchos</i>), Great tit (<i>Parus major</i>), Japanese Tit (<i>Parus minor</i>), Oriental skylark (<i>Alauda gulgula</i>), Zitting cisticola (<i>Cisticola juncidis</i>), Hill prinia (<i>Prinia supercilialis</i>), Yellow-bellied prinia (<i>Prinia flaviventris</i>), Plain prinia (<i>Prinia inornate</i>), Common Tailorbird (<i>Orthotomus sutorius</i>), Pygmy wren babbler (<i>Pnoepyga pusilla</i>), Swallow (<i>Hirundo rustica</i>), Red-rumped swallow (<i>Cecropis daurica</i>), Red-whiskered bulbul (<i>Pycnonotus jocosus</i>), Light-vented bulbul (<i>Pycnonotus sinensis</i>), Sooty-headed bulbul (<i>Pycnonotus aurigaster</i>), Chestnut bulbul (<i>Hemixos castanonotus</i>), Black bulbul (<i>Hypsipetes leucocephalus</i>), Dusky warbler (<i>Phylloscopus fuscatus</i>), Yellow-rumped willow warbler (<i>Phylloscopus proregulus</i>), Yellow-browed willow warbler (<i>Phylloscopus inornatus</i>), Hume's leaf-warbler (<i>Phylloscopus humei</i>), Pale-footed bush-warbler (<i>Hemitesia pallidipes</i>), Brownish-flanked bush-warbler (<i>Horornis fortipes</i>), Black-throated tit (<i>Aegithalos concinnus</i>), Chestnut-flanked white-eye (<i>Zosterops erythropleurus</i>), Japanese white-eye (<i>Zosterops japonicus</i>), Streak-breasted scimitar-babbler (<i>Pomatorhinus ruficollis</i>), Red-headed tree babbler (<i>Stachyris ruficeps</i>), Grey-cheeked fulvetta (<i>Alcippe morrisonia</i>), Babbler (<i>Garrulax canorus</i>), Masked Laughingthrush (<i>Garrulax perspicillatus</i>), Crested myna (<i>Acridotheres cristatellus</i>), Red-billed starling (<i>Sturnus sericeus</i>), White-cheeked Starling (<i>Sturnus cineraceus</i>), Black-collared starling (<i>Sturnus nigricollis</i>), White-shouldered starling (<i>Sturnia sinensis</i>), Scaly thrush (<i>Zoothera aurea</i>), Grey-backed thrush (<i>Turdus hortolorum</i>), Eurasian blackbird (<i>Turdus merula</i>), Siberian rubythroat (<i>Calliope calliope</i>), Oriental magpie-robin (<i>Copsychus saularis</i>), Common shama thrush (<i>Kittacinacla malabarica</i>), Daurian Redstart (<i>Phoenicurus aureus</i>), Plumbeous water-redstart (<i>Rhyacornis fuliginosus</i>), Stonechat (<i>Saxicola torquatus</i>), Amur stonechat (<i>Saxicola stejnegeri</i>), Chestnut-bellied rock thrush (<i>Monticola rufiventris</i>), Asian brown flycatcher (<i>Muscicapa dauurica</i>), Fork-tailed sunbird (<i>Aethopyga latouchii</i>), White-rumped munia (<i>Lonchura striata</i>), Scaly-breasted munia (<i>Lonchura punctulata</i>), Tree sparrow (<i>Passer montanus</i>), Yellow wagtail (<i>Motacilla tschutschensis</i>), Grey Wagtail (<i>Motacilla cinerea</i>), White wagtail (<i>Motacilla alba</i>), Richard's pipit (<i>Anthus richardi</i>), Olive-backed pipit (<i>Anthus hodgsoni</i>), Anthus cervinus (<i>Anthus cervinus</i>), Meadow bunting (<i>Emberiza cioides</i>), Chestnut-eared bunting (<i>Emberiza fucata</i>), Little bunting (<i>Emberiza pusilla</i>), Black-faced bunting (<i>Emberiza spodocephala</i>).
Wading bird	Eastern water rail (<i>Rallus indicus</i>), Marsh Crake (<i>Porzana pusilla</i>), White-breasted waterhen (<i>Amaurornis phoenicurus</i>), Brown crake (<i>Amaurornis akool</i>), Common moorhen (<i>Gallinula chloropus</i>), Common coot (<i>Fulica atra</i>), Eurasian Oystercatcher (<i>Haematopus ostralegus</i>), Ibisbill (<i>Ibidorhyncha struthersii</i>), Black-winged stilt (<i>Himantopus Himantopus</i>), Pied Avocet (<i>Recurvirostra avosetta</i>), Grey-headed lapwing (<i>Vanellus cinereus</i>), Pacific golden plover (<i>Pluvialis fulva</i>), Grey plover (<i>Pluvialis squatarola</i>), Little ringed plover (<i>Charadrius dubius</i>), Kentish plover (<i>Charadrius alexandrinus</i>), Lesser sand plover (<i>Charadrius mongolus</i>), Greater sand plover (<i>Charadrius leschenaultia</i>), Common sandpiper (<i>Actitis hypoleucos</i>), Swinhoe's snipe (<i>Gallinago megala</i>), Common snipe (<i>Gallinago gallinago</i>), Black-tailed godwit (<i>Limosa limosa</i>), Bar-tailed Godwit (<i>Limosa lapponica</i>), Whimbrel (<i>Numenius phaeopus</i>), Eurasian curlew (<i>Numenius Arquata</i>), Far eastern curlew (<i>Numenius madagascariensis</i>), Spotted redshank (<i>Tringa erythropus</i>), Common redshank (<i>Tringa tetanus</i>), Marsh sandpiper (<i>Tringa stagnatilis</i>), Common greenshank (<i>Tringa nebularia</i>), Spotted greenshank (<i>Tringa guttifer</i>), Green sandpiper (<i>Tringa ochropus</i>), Wood sandpiper (<i>Tringa glareola</i>), Great knot (<i>Calidris tenuirostris</i>), Sanderling (<i>Calidris alba</i>), Red-necked stint (<i>Calidris ruficollis</i>), Spoon-billed sandpiper (<i>Euryorhynchus pygmeus</i>), Temminck's Stint (<i>Calidris temminckii</i>), Curlew Sandpiper (<i>Calidris ferruginea</i>), Dunlin (<i>Calidris alpina</i>), Red knot (<i>Calidris canutus</i>), Red-necked phalarope (<i>Phalaropus lobatus</i>), Oriental pratincole (<i>Glareola maldivarum</i>), Oriental white stork (<i>Ciconia boyciana</i>), Great cormorant (<i>Phalacrocorax carbo</i>), Pelagic cormorant (<i>Phalacrocorax Pelagicus</i>), Eastern white pelican (<i>Pelecanus onocrotalus</i>), Eurasian spoonbill (<i>Platalea leucorodia</i>), Black-faced spoonbill (<i>Platalea minor</i>), Yellow bittern (<i>Ixobrychus sinensis</i>), Cinnamon bittern (<i>Ixobrychus cinnamomeus</i>), Black-crowned night-heron (<i>Nycticorax nycticorax</i>), Striated heron (<i>Butorides striata</i>), Chinese pond-heron (<i>Ardeola bacchus</i>), Cattle egret (<i>Bubulcus ibis</i>), Grey heron (<i>Ardea cinerea</i>), Purple heron (<i>Ardea purpurea</i>), Great egret (<i>Ardea alba</i>), Intermediate egret (<i>Ardea intermedia</i>), Little egret (<i>Egretta garzetta</i>), Chinese egret (<i>Egretta eulophotes</i>).
Swimming bird	Bean goose (<i>Anser fabalis</i>), Tundra swan (<i>Cygnus columbianus</i>), Common shelduck (<i>Tadorna tadorna</i>), Ruddy shelduck (<i>Tadorna ferruginea</i>), Gadwall (<i>Anas strepera</i>), Anas penelope (<i>Anas Penelope</i>), Common mallard (<i>Anas platyrhynchos</i>), Eastern spot-billed duck (<i>Anas zonorhyncha</i>), Northern pintail (<i>Anas acuta</i>), Common teal (<i>Anas crecca</i>), Northern shoveler (<i>Anas clypeata</i>), Garganey (<i>Spatula querquedula</i>), Baikal teal (<i>Sibirionetta Formosa</i>), Greater scaup (<i>Aythya marila</i>), Tufted duck (<i>Aythya fuligula</i>), Little grebe (<i>Tachybaptus ruficollis</i>), Great crested grebe (<i>Podiceps cristatus</i>), Black-headed gull (<i>Larus ridibundus</i>), Saunders's gull (<i>Larus saundersi</i>), Black-tailed gull (<i>Larus crassirostris</i>), Little tern (<i>Sterna albifrons</i>), Hydroprogne caspia (<i>Hydroprogne caspia</i>), Common tern (<i>Sterna hirundo</i>), Whiskered tern (<i>Chlidonias hybrida</i>), White-winged tern (<i>Chlidonias leucopterus</i>), Black tern (<i>Chlidonias niger</i>).
Climbing bird	Fork-tailed swift (<i>Apus pacificus</i>), Little swift (<i>Apus nipalensis</i>), Paradoxornis brunneus (<i>Centropus sinensis</i>), Lesser coucal (<i>Centropus bengalensis</i>), Asian koel (<i>Eudynamis scolopaceus</i>), Surniculus lugubris (<i>Surniculus lugubris</i>), Indian cuckoo (<i>Cuculus Micropterus</i>), Green-billed malkoha (<i>Phaenicophaeus tristis</i>), Common hoopoe (<i>Upupa epops</i>), Blue-tailed bee-eater (<i>Merops philippinus</i>), Ruddy kingfisher (<i>Halcyon coromanda</i>), White-breasted kingfisher (<i>Halcyon smyrnensis</i>), Black-capped kingfisher (<i>Halcyon pileate</i>), Common kingfisher (<i>Alcedo atthis</i>), Crested kingfisher (<i>Ceryle rudis</i>), Eurasian wryneck (<i>Jynx torquilla</i>), Chinese penduline-tit (<i>Remiz consobrinus</i>).
Raptor	Osprey (<i>Pandion haliaetus</i>), Black-winged kite (<i>Elanus caeruleus</i>), Crested goshawk (<i>Accipiter trivirgatus</i>), Chinese sparrowhawk (<i>Accipiter soloensis</i>), Besra (<i>Accipiter virgatus</i>), Pallid harrier (<i>Circus spilonotus</i>), Black kite (<i>Milvus migrans</i>), Crested serpent-eagle (<i>Spilornis cheela</i>), Common kestrel (<i>Falco tinnunculus</i>), Eurasian hobby (<i>Falco Subbuteo</i>).
Terrestrial bird	Common pheasant (<i>Phasianus colchicus</i>), Oriental turtle-dove (<i>Streptopelia orientalis</i>), Collared turtle dove (<i>Streptopelia tranquebarica</i>), Spotted dove (<i>Spilopelia chinensis</i>), Barred cuckoo-dove (<i>Macropygia unchall</i>).

(1) Songbirds. The importance of factors driving songbird diversity, such as mangrove area, aquaculture pond area, COD, mudflat area, water body area, and soil salinity, is evident from Figure 2B and Table 6, particularly in terms of the degree of impact of simple effects. The interpretation rates of these factors were 97.2%, 80.4%, 73.9%, 53.2%, 39.8%, 21.1%, and 14.4%, respectively.

Among these, mangroves stood out as the primary driver, with an interpretation rate of 97.2%. Therefore, mangrove areas played a crucial role in the conservation of songbird diversity.

(2) Wading birds. In terms of the impact of simple effects, Figure 2C and Table 6 illustrate that the aquaculture pond area, mangrove area, mudflat area, and water body area significantly

TABLE 4 Characteristics of driving factors.

Variable	Min	Max	Mean \pm SE
Crown breadth(cm)	121.8	1070.6	380.8 \pm 271.8
Number of mangrove species	1	8	3.70 \pm 2.02
The proportion of native species (%)	0	100.00	65.58 \pm 30.33
Mangrove area (ha)	1	4241	303.56 \pm 933.36
Mudflat (ha)	1	5055	845.69 \pm 1368.10
Aquaculture pond area (ha)	0	6604	604.83 \pm 1589.97
Water body area (ha)	1	5171	860.59 \pm 1491.46
pH	7.62	9.94	8.09 \pm 0.52
Temperature (°C)	21.17	26.75	24.46 \pm 1.27
Salinity (%)	0.15	2.93	1.00 \pm 0.73
Dissolved oxygen (mg/L)	24.46	53.91	38.98 \pm 8.73
COD (mg/L)	55.91	394.22	132.55 \pm 70.37
Sulfide (mg/L)	0.01	0.28	0.057 \pm 0.057
Nitrite (mg/L)	0.02	0.22	0.061 \pm 0.044
Ammonia (mg/L)	0.32	6.48	1.67 \pm 1.49
Organic carbon (%)	0.22	2.36	0.96 \pm 0.52
Suspended matter (%)	7.60	128.04	50.89 \pm 28.96
Inorganic phosphate (mg/L)	0.01	2.90	0.35 \pm 0.62
Reactive silicate (mg/L)	1.00	5.96	3.29 \pm 1.42

influenced the diversity of wading birds. Specifically, aquaculture pond areas, mangrove areas, mudflat areas, and water body areas had interpretation rates of 50.9%, 49.9%, 34.8%, and 28.1%, respectively. In terms of their impact on conditional effects, the aquaculture pond area stood out as the primary driver, with an interpretation rate of 50.9%. Hence, the aquaculture pond area was pivotal in driving bird diversity and plays a significant role in this regard.

(3) Swimming birds. As shown in Figure 2D and Table 6, the aquaculture pond area, mangrove area, mudflat area, and water body area significantly contributed to the diversity of swimming birds in terms of their degree of impact on simple effects. The interpretation rates of these factors were 73.7%, 67.3%, 42.5%, and 24.5%, respectively. Regarding conditional effects, the aquaculture pond area emerged as the primary driver, with an interpretation rate of 73.7%. Thus, the aquaculture pond area was a key factor affecting the diversity of swimming birds.

(4) Climbing birds. As shown in Figure 2E and Table 6, mangrove area, aquaculture pond area, COD, mudflat area, and number of mangrove species significantly contributed to the diversity of climbing birds in terms of their degree of impact on simple effects. The interpretation rates of these factors were 55.8%,

53.7%, 42.1%, 34.4%, and 10.9%, respectively. Regarding conditional effects, the mangrove area emerged as the main driver, with an interpretation rate of 55.8%. Therefore, the mangrove area was a key factor influencing the diversity of climbing birds and plays a crucial role in their conservation efforts.

(5) Raptors. As shown in Figure 2F and Table 6, the mangrove area and aquaculture pond area were the main drivers of raptor diversity in terms of the impact degree of simple effects. The interpretation rates of these factors were 24.5%, 19.5%, and 12.7%, respectively. Regarding conditional effects, the mangrove area stood out as the main driver, with an interpretation rate of 24.5%. Although the mangrove area was the primary factor influencing raptor diversity, its contribution was comparatively lower than that of other types of bird diversity.

(6) Terrestrial birds. As shown in Figure 2G and Table 6, the mangrove area, COD, aquaculture pond area, and mudflat area were the primary drivers of terrestrial bird diversity in terms of their degree of impact on simple effects. The interpretation rates of these factors were 32.0%, 28.7%, 27.6%, and 19.9%, respectively. Regarding conditional effects, the mangrove area emerged as the main driver, with an interpretation rate of 32.0%. Thus, the mangrove area was the primary factor influencing terrestrial bird diversity, although its contribution was relatively lower than that of other types of bird diversity.

In summary, the influence of specific driving factors on the diversity of different types of birds varies. Overall, mangrove areas emerged as the primary driving factor for land-dwelling birds, such as songbirds, climbing birds, raptors, and terrestrial birds, whereas the aquaculture pond area significantly affected water birds such as wading birds and swimming birds. Additionally, the water area, mudflat area, and other factors also play crucial roles in shaping bird diversity.

4 Discussion

4.1 Areas of aquaculture ponds, mangroves, and mudflats are important factors driving the diversity of birds

This study examined the impact of driving factors, such as mangrove habitat landscape factors, mangrove community structure, water environment, and soil sedimentary environment, on bird diversity. RA revealed that the areas of aquaculture ponds, mangroves, and mudflats significantly affected bird diversity, with interpretation rates of 31.0%, 28.9%, and 20.3%, respectively. Therefore, these factors were crucial for maintaining bird diversity.

Aquaculture pond areas can significantly affect bird diversity. Although some studies have indicated that large-scale coastal aquaculture pond construction can occupy bird habitats and reduce diversity levels (Zhang and Ouyang, 2019), others have suggested that these ponds can serve as important bird habitats (Yasué and Dearden, 2009; Lehnen and Kremenetz, 2013; Navedo et al., 2013; Fonseca and Navedo, 2020) and supplementary foraging sites (Walton et al., 2015; Wei et al., 2017; Fonseca and

TABLE 5 RA ranking results between bird communities and environmental factors.

Guild	Statistic	Axis				Explanatory variables account	Adjusted explained variation
		Axis1	Axis2	Axis3	Axis4		
All birds	Eigenvalues	0.3597	0.1282	0.0731	0.0473	73.2%	49.1%
	Explained variation (cumulative)	35.97	48.79	56.11	60.84		
	Pseudo-canonical correlation (suppl.)	0.9807	0.9248	0.9862	0.9244		
	Explained fitted variation (cumulative)	49.13	66.64	76.63	83.10		
Songbird	Eigenvalues	0.9869	0.0043	0.0013	0.0006	99.4%	98.8%
	Explained variation (cumulative)	98.69	99.12	99.25	99.32		
	Pseudo-canonical correlation (suppl.)	0.9991	0.9040	0.7314	0.8313		
	Explained fitted variation (cumulative)	99.30	99.74	99.87	99.94		
Wading bird	Eigenvalues	0.5788	0.2743	0.0541	0.0081	92.3%	86.7%
	Explained variation (cumulative)	57.88	85.31	90.72	91.53		
	Pseudo-canonical correlation (suppl.)	0.9904	0.9297	0.8854	0.9402		
	Explained fitted variation (cumulative)	62.70	92.43	98.28	99.16		
Swimming bird	Eigenvalues	0.8316	0.0540	0.0085	0.0050	90.0%	84.2%
	Explained variation (cumulative)	83.16	88.56	89.41	89.91		
	Pseudo-canonical correlation (suppl.)	0.9732	0.7994	0.9153	0.5373		
	Explained fitted variation (cumulative)	92.39	98.38	99.33	99.88		
Climbing bird	Eigenvalues	0.5961	0.0496	0.0473	0.0226	72.0%	59.1%
	Explained variation (cumulative)	59.61	64.57	69.30	71.57		
	Pseudo-canonical correlation (suppl.)	0.9868	0.6501	0.8074	0.6997		
	Explained fitted variation (cumulative)	82.78	89.66	96.23	99.37		
Raptor	Eigenvalues	0.4230	0.2484	0.0548	0.0279	79.6%	61.3%
	Explained variation(cumulative)	42.30	67.14	72.62	75.41		
	Pseudo-canonical correlation (suppl.)	0.9330	0.9698	0.9697	0.7367		
	Explained fitted variation (cumulative)	53.12	84.32	91.21	94.71		
Terrestrial bird	Eigenvalues	0.4720	0.0997	0.0217	0.0099	60.4%	42.1%
	Explained variation (cumulative)	47.20	57.17	59.34	60.33		
	Pseudo-canonical correlation (suppl.)	0.8541	0.6303	0.6814	0.5783		
	Explained fitted variation (cumulative)	78.17	94.69	98.28	99.93		

Navedo, 2020; Wang et al., 2020). This may be because birds can access high-energy food resources in aquaculture ponds (Mander et al., 2007; Ehmke et al., 2016). Different from profit-driven aquaculture pond construction within mangrove forests (Van et al., 2015), aquaculture ponds within naturally protected areas prioritize ecological benefits over economic gains. In China, the government has repurposed aquaculture ponds within protected areas, utilizing them as supplemental habitats, exchanging fish resources through tidal activity (Yang et al., 2022), or providing annual fish and shrimp supplements to sustain bird diversity. For example, the Guangdong Haifeng Avian Natural Reserve

conserves nearly 90% of its tidal exchange ponds, and attracts over 300 bird species and 40,000 birds annually. Similarly, the Zhuhai Qi'ao-Dangan Island Provincial Nature Reserve has converted portions of its *Sonneratia apetala* forest into aquaculture ponds to attract geese, ducks, and herons. Therefore, in managing mangrove ecosystems, it is essential to preserve mangrove vegetation, beaches, water, and aquaculture ponds. These ponds should be retained through leasing or redemption and utilized to facilitate the exchange of aquatic biological resources with the tide. This approach enhances the foraging grounds available to the birds.

Mangrove areas can significantly influence bird diversity, serving as vital ecosystems for breeding, inhabiting, and feeding on numerous bird species. However, the extent of habitat utilization depends on mangrove area and vegetation structure (Mancini et al., 2018). Our findings revealed a close correlation between mangrove bird diversity and mangrove area, with mangrove community structure, such as species count, crown width and proportion of native species, making a relatively modest contribution to bird diversity. China has experienced mangrove destruction, protection, and restoration. Despite efforts to restore mangrove ecosystem functions by planting native species in natural protected areas, over 80% of

restored mangroves remain as degraded secondary forests (Sui and Zhang, 2001). Consequently, the mangrove community structure remains relatively simple, with limited contribution to bird diversity. Mangroves play pivotal roles in driving bird diversity. As mangrove cover areas expand, bird diversity increases (Zou et al., 2008), fostering three-dimensional complex habitats owing to larger patch areas, that offer diverse microhabitats (Jo et al., 2012; Jayasilan et al., 2015) and ecological niches, thus enhancing niche heterogeneity and accommodating various bird breeding and habitat needs (Chen et al., 2017; Mancini et al., 2018). To further bolster biodiversity, the Chinese government plans to expand mangrove planting in

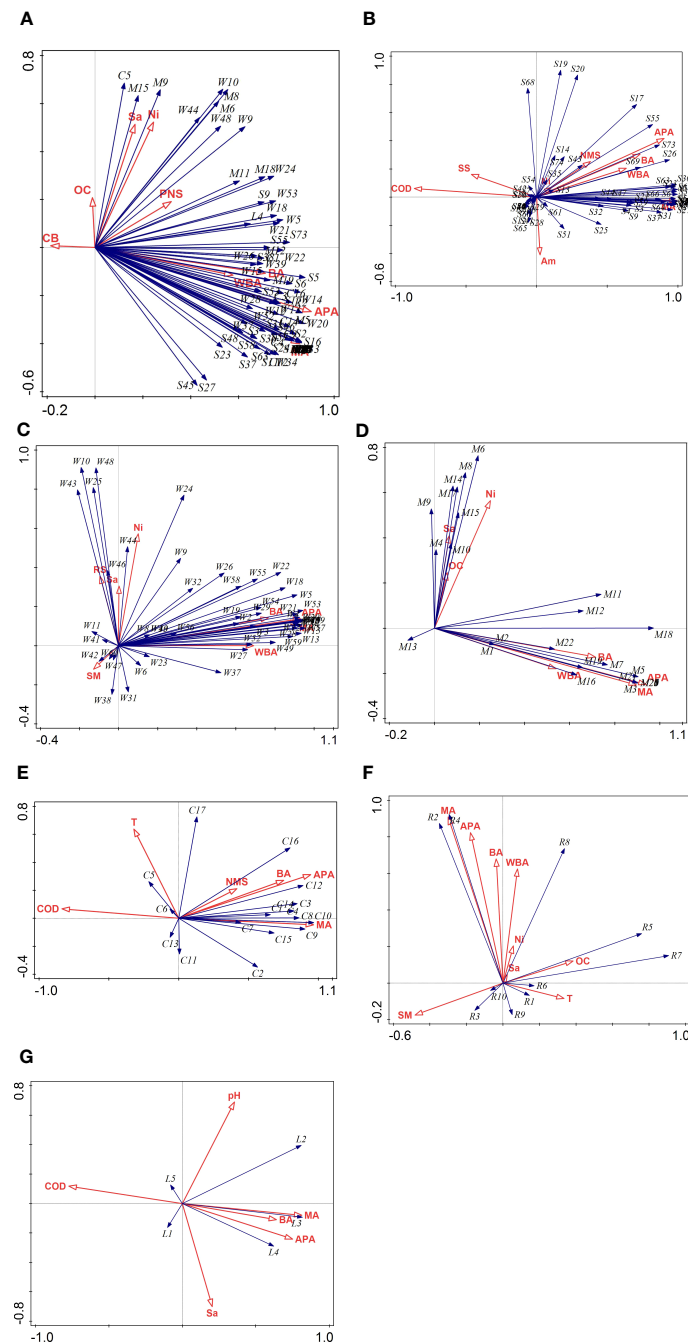


FIGURE 2 (Continued)

FIGURE 2 (Continued)

Relationships between birds and habitat characteristics. (A) All birds, (B) Songbird, (C) Wading bird, (D) Swimming bird, (E) Climbing bird, (F) Raptor, (G) Terrestrial bird. Explanatory variables: CB, Crown breadth (cm); NMS, Number of mangrove species; PNS, Proportion of native species (%); MA, Mangrove area (ha); BA, Mudflat (ha); APA, Aquaculture pond area(ha); WBA, Water body area(ha); T, Temperature (°C); Sa, Salinity (%); SS, Soil salinity (%FS); COD, (mg/L); Ni, Nitrate (mg/L); OC, Organic carbon (%); SM, Suspended matter (%); RS, Reactive silicate (mg/L). Songbirds: S1-*Pericrocotus divaricatus*, S2-*Dicrurus macrocercus*, S3-*Dicrurus hottentottus*, S4-*Lanius cristatus*, S5-*Lanius Schach*, S6-*Lanius tephronotus*, S7-*Garrulus glandarius*, S8-*Cyanopica cyanus*, S9-*Urocissa erythrorhyncha*, S10-*Dendrocitta formosae*, S11-*Pica pica*, S12-*Corvus pectoralis*, S13-*Corvus macrorhynchos*, S14-*Parus major*, S15-*Parus minor*, S16-*Alauda gulgula*, S17-*Cisticola juncidis*, S18-*Prinia supercilii*, S19-*Prinia flaviventris*, S20-*Prinia inornata*, S21-*Orthotomus sutorius*, S22-*Pnoepyga pusilla*, S23-*Hirundo rustica*, S24-*Cecropis daurica*, S25-*Pycnonotus jocosus*, S26-*Pycnonotus sinensis*, S27-*Pycnonotus aurigaster*, S28-*Hemixos castanonotus*, S29-*Hypsipetes leucocephalus*, S30-*Phylloscopus fuscatus*, S31-*Phylloscopus proregulus*, S32-*Phylloscopus inornatus*, S33-*Phylloscopus humei*, S34-*Hemitesia pallidipes*, S35-*Horornis fortipes*, S36-*Aegithalos concinnus*, S37-*Zosterops erythropleurus*, S38-*Zosterops japonicus*, S39-*Pomatorhinus ruficollis*, S40-*Stachyris ruficeps*, S41-*Alcippe morrisonia*, S42-*Garrulax canorus*, S43-*Garrulax perspicillatus*, S44-*Acridotheres cristatellus*, S45-*Sturnus sericeus*, S46-*Sturnus cineraceus*, S47-*Sturnus nigricollis*, S48-*Sturnia sinensis*, S49-*Zoothera aurea*, S50-*Turdus hortulorum*, S51-*Turdus merula*, S52-*Calliope calliope*, S53-*Copsychus saularis*, S54-*Kittacincla malabarica*, S55-*Phoenicurus aureus*, S56-*Rhyacornis fuliginosus*, S57-*Saxicola torquatus*, S58-*Saxicola stejnegeri*, S59-*Monticola rufiventris*, S60-*Muscicapa daurica*, S61-*Aethopyga latouchii*, S62-*Lonchura striata*, S63-*Lonchura punctulata*, S64-*Passer montanus*, S65-*Motacilla tschutschensis*, S66-*Motacilla cinerea*, S67-*Motacilla alba*, S68-*Anthus richardi*, S69-*Anthus hodgsoni*, S70-*Anthus cervinus*, S71-*Emberiza coides*, S72-*Emberiza fucata*, S73-*Emberiza pusilla*, S74-*Emberiza spodocephala*. Wading birds: W1-*Rallus indicus*, W2-*Porzana pusilla*, W3-*Amaurornis phoenicurus*, W4-*Amaurornis akool*, W5-*Gallinula chloropus*, W6-*Fulica atra*, W7-*Haematopus ostralegus*, W8-*Ibidorhyncha struthersii*, W9-*Himantopus himantopus*, W10-*Recurvirostra avosetta*, W11-*Vanellus cinereus*, W12-*Pluvialis fulva*, W13-*Pluvialis squatarola*, W14-*Charadrius dubius*, W15-*Charadrius alexandrinus*, W16-*Charadrius mongolus*, W17-*Charadrius leschenaultia*, W18-*Actitis hypoleucos*, W19-*Gallinago megal*, W20-*Gallinago gallinago*, W21-*Limosa limosa*, W22-*Limosa lapponica*, W23-*Numenius phaeopus*, W24-*Numenius Arquata*, W25-*Numenius madagascariensis*, W26-*Tringa erythropus*, W27-*Tringa tetanus*, W28-*Tringa stagnatilis*, W29-*Tringa nebularia*, W30-*Tringa guttifer*, W31-*Tringa ochropus*, W32-*Tringa glareola*, W33-*Calidris tenuirostris*, W34-*Calidris alba*, W35-*Calidris ruficollis*, W36-*Euryrhyngchus pygmeus*, W37-*Calidris temminckii*, W38-*Calidris ferruginea*, W39-*Calidris alpina*, W40-*Calidris canutus*, W41-*Phalaropus lobatus*, W42-*Glareola maldivarum*, W43-*Ciconia boyciana*, W44-*Phalacrocorax carbo*, W45-*Phalacrocorax Pelagicus*, W46-*Pelecanus onocrotalus*, W47-*Platalea leucorodia*, W48-*Platalea minor*, W49-*Ixobrychus sinensis*, W50-*Ixobrychus cinnamomeus*, W51-*Nycticorax nycticorax*, W52-*Butorides striata*, W53-*Ardeola bacchus*, W54-*Bubulcus ibis*, W55-*Ardea cinerea*, W56-*Ardea purpurea*, W57-*Ardea alba*, W58-*Ardea intermedia*, W59-*Egretta garzetta*, W60-*Egretta eulophotes*. Swimming birds: M1-*Anser fabalis*, M2-*Cygnus columbianus*, M3-*Tadorna tadorna*, M4-*Tadorna ferruginea*, M5-*Anas strepera*, M6-*Anas Penelope*, M7-*Anas platyrhynchos*, M8-*Anas zonorhyncha*, M9-*Anas acuta*, M10-*Anas crecca*, M11-*Anas clypeata*, M12-*Spatula querquedula*, M13-*Sibirionetta Formosa*, M14-*Aythya marila*, M15-*Aythya fuligula*, M16-*Tachybaptus ruficollis*, M17-*Podiceps cristatus*, M18-*Larus ridibundus*, M19-*Larus saundersi*, M20-*Larus crassirostris*, M21-*Sterna albifrons*, M22-*Hydroprogne caspia*, M23-*Sterna hirundo*, M24-*Chlidonias hybrida*, M25-*Chlidonias leucopterus*, M26-*Chlidonias niger*, M27-*Chlidonias hybrida*. Climbing birds: C1-*Apus pacificus*, C2-*Apus nipalensis*, C3-*Centropus sinensis*, C4-*Centropus bengalensis*, C5-*Eudynamis scolopaceus*, C6-*Surniculus lugubris*, C7-*Cuculus Micropterus*, C8-*Phaenicophaeus tristis*, C9-*Upupa epops*, C10-*Merops philippinus*, C11-*Halcyon coromanda*, C12-*Halcyon smyrnensis*, C13-*Halcyon pileate*, C14-*Alcedo atthis*, C15-*Ceryle rudis*, C16-*Jynx torquilla*, C17-*Remiz consobrinus*. Raptors: R1-*Pandion haliaetus*, R2-*Elanus caeruleus*, R3-*Accipiter trivirgatus*, R4-*Accipiter soloensis*, R5-*Accipiter virgatus*, R6-*Circus spilonotus*, R7-*Milvus migrans*, R8-*Spilornis cheela*, R9-*Falco tinnunculus*, R10-*Falco Subbuteo*. Terrestrial birds: L1-*Phasianus colchicus*, L2-*Streptopelia orientalis*, L3-*Streptopelia tranquebarica*, L4-*Spilopelia chinensis*, L5-*Macropygia unchall*.

naturally protected areas through initiatives such as *A Specific Project for the Protection and Restoration of Mangroves* (2020–2025). For example, the Zhuhai Qi'ao-Dangan Island Provincial Nature Reserve intends to plant 50 ha of mangroves in 2023 to maintain high biodiversity levels. Notably, in the Zhanjiang Mangrove National Nature Reserve, extensive mangrove planting efforts have corresponded to an upward trend in bird diversity (Li et al., 2013).

Mudflat areas have emerged as the main factor affecting bird diversity. Existing research confirms that mudflats offer abundant food resources for birds (Burger, 2018), with larger areas harboring more benthic organisms and better resistance to declines in benthic animal density owing to bird foraging (Fonseca et al., 2017). Particularly during low tides, mudflats provide optimal foraging conditions, as more invertebrates become accessible (Jimenez et al., 2015). Despite serving as a vital foraging ground for birds in protected areas, managing mudflats in these areas poses new challenges. For instance, in some protected areas, non-forest lands, including aquaculture ponds, mudflats, and shallow water areas, are being converted into large-scale mangrove planting areas, encroaching on bird foraging grounds and subsequently diminishing bird diversity levels. Consequently, the scientific management of mangrove areas remains an area of ongoing investigation and discussion.

The water area, environmental factors, and soil sedimentary environments contribute to bird diversity to some extent. Water

areas significantly affect waterfowls, such as geese, ducks, gulls, and herons, providing essential elements such as varied water levels, hiding conditions, and food sources (Yang et al., 2022). However, its influence on terrestrial birds was comparatively limited (Table 6 and Figure 2). Despite the relatively weak response of birds to water and soil environments, this does not mean that their effect on bird diversity is insignificant. Previous studies have indicated that water quality (Caussy, 2009) and soil sediment conditions (Weinstein and Daniel, 2002; Cannicci et al., 2008) affect bird diversity by influencing benthic organism diversity. Certain waterfowl species, such as loons and large wading birds, thrive at moderate salinity levels (20–40 ppt), with abundance declining sharply beyond 100 ppt, as high salinity can lead to rapid dehydration and compromise feather waterproofing. Soil organic matter content correlates with the abundance of species such as crabs (Cannicci et al., 2008), which are vital food sources for certain birds. Further research is required to fully understand the effects of these factors on bird diversity.

4.2 Driving factors of diversity in different types of birds

The impact of specific driving factors on different bird types varied. However, mangrove areas have emerged as the primary driver for land-dwelling birds such as songbirds, climbers, raptors,

TABLE 6 Simple effects and conditional effects of birds.

Guild	Simple Effects				Conditional Effects			
	Factor	Explains (%)	Pseudo-F	P	Factor	Explains (%)	Pseudo-F	P
All birds	APA	31.0	8.1	0.002	APA	31.0	8.1	0.002
	MA	28.9	7.3	0.032	MA	7.8	2.2	0.056
	BA	20.3	4.6	0.010	Ni	5.6	1.6	0.088
	WBA	15.1	3.2	0.034	Sa	7.1	2.2	0.030
					PNS	5.1	1.6	0.080
					CB	5.6	1.9	0.042
					OC	4.3	1.6	0.082
Songbird	MA	97.2	616	0.014	MA	97.2	616	0.020
	APA	80.4	73.7	0.002	APA	0.8	7.2	0.036
	COD	73.9	51.1	0.046	NMS	0.5	5.2	0.014
	BA	53.2	20.4	0.008	BA	0.2	2.7	0.058
	WBA	39.8	11.9	0.064	WBA	0.4	5.7	0.040
	SS	21.1	4.8	0.032	Ni	0.1	2.5	0.064
	NMS	14.4	3.0	0.070				
Wading bird	APA	50.9	18.7	0.004	APA	50.9	18.7	0.002
	MA	49.9	17.9	0.032	Ni	9.2	3.9	0.024
	BA	34.8	9.6	0.006	SM	5.8	2.7	0.068
	WBA	28.1	7.0	0.028	Sa	4.8	2.5	0.074
					MA	5.8	3.5	0.066
					RS	5.3	3.8	0.063
					WBA	5.5	5.2	0.044
					BA	4.9	7.0	0.006
Swimming bird	APA	73.7	50.6	0.008	APA	73.7	50.6	0.006
	MA	67.3	37.0	0.028	OC	5.2	4.2	0.034
	BA	42.5	13.3	0.012	Ni	4.9	4.8	0.012
	WBA	24.5	5.9	0.064				
Climbing bird	MA	55.8	22.7	0.016	MA	55.8	22.7	0.008
	APA	53.7	20.9	0.002	APA	7.0	3.2	0.082
	COD	42.1	13.1	0.030	T	5.5	2.8	0.044
	BA	34.4	9.5	0.018				
	NMS	10.9	2.2	0.096				
Raptor	MA	24.5	5.8	0.094	MA	24.5	5.8	0.068
	APA	19.5	4.4	0.092	SM	11.1	2.9	0.068
	BA	12.7	2.6	0.090	WBA	7.6	2.1	0.166
					OC	8.9	2.8	0.048
					Sa	7.7	2.7	0.052
					APA	8.4	3.4	0.040
					BA	5.2	2.3	0.062

(Continued)

TABLE 6 Continued

Guild	Simple Effects				Conditional Effects			
Terrestrial bird	MA	32.0	8.5	0.026	MA	32.0	8.5	0.020
	COD	28.7	7.2	0.022	pH	13.9	4.4	0.070
	APA	27.6	6.9	0.014	Sa	10.8	4.0	0.036
	BA	19.9	4.5	0.030				

Explanatory variables: CB, Crown breadth (cm); NMS, Number of mangrove species; PNS, Proportion of native species (%); MA, Mangrove area (ha); BA, Mudflat (ha); APA, Aquaculture pond area (ha); WBA, Water body area (ha); T, Temperature (°C); Sa, Salinity (%); SS, Soil salinity (%FS); COD, COD (mg/L); Ni, Nitrate (mg/L); OC, Organic carbon (%); SM, Suspended matter (%); and RS, Reactive silicate (mg/L).

and terrestrial birds, whereas aquaculture pond areas predominate for water birds such as wading birds and swimming birds. Various bird types exhibit distinct responses to these driving factors and are influenced by specific ecological considerations.

(1) Mangrove areas can significantly affect the diversity of songbirds, climbing birds, raptors, terrestrial birds, and other land-dwelling bird species.

The extent of mangrove areas typically determines the internal or marginal effects within mangrove ecosystems (Li et al., 2013), profoundly influencing the diversity of birds inhabiting mangroves, including songbirds, climbing birds, raptors, and terrestrial birds. Larger patches of mangroves play a more crucial role in reducing fragmentation and isolation between patches, than smaller patches do. Small mangrove areas may hinder communication among mangrove organisms, particularly by affecting ground-nesting birds, such as terrestrial birds (Uezu et al., 2005). Conversely, larger mangrove areas encompass a greater variety of mangrove species and support diverse mangrove communities, catering to the breeding, roosting, foraging, and hiding requirements of terrestrial birds (Jo et al., 2012; Jayasilan et al., 2015). Moreover, the complex structure of mangrove communities promotes the growth of benthic organisms and insects (Cannicci et al., 2008), which are essential components of the food chain in mangrove ecosystems. The increased biomass of these organisms enhances bird diversity (Hamza et al., 2015). For example, in the Zhanjiang Mangrove National Nature Reserve, a decline in the mangrove area led to a sharp decrease in falcon and eagle populations, highlighting the role of mangrove areas in raptor decline. After the restoration of extensive mangrove areas, populations of songbirds, such as *Sternus nigricollis* increased by 10%–20%, and populations of *Streptopelia chinensis* increased by approximately 30% (Li et al., 2013). This evidence demonstrates the importance of expanding mangrove plantations within protected areas to support terrestrial bird populations.

(2) Aquaculture ponds play a pivotal role in driving waterbirds, particularly wading and swimming birds.

Aquaculture ponds serve as important habitats for maintaining the diversity of water birds, including wading and swimming species (Mander et al., 2007; Ehmke et al., 2016), and as supplements or alternatives to natural foraging grounds. Currently, aquaculture ponds within natural mangrove protected areas in Guangdong Province have transitioned from economic to ecological significance. Owing to factors such as body size, beak length, and leg length, wading and swimming birds exhibit varied

preferences for using these ponds. Studies have indicated that small shorebirds prefer water depths below 5 cm, large shorebirds between 5 cm–10 cm, geese and ducks between 10 cm–15 cm, diving ducks over 20 cm, and herons between 0 cm–30 cm (Therkildsen and Bregnballe, 2006). Consequently, the Guangzhou Nansha Wetland Park, Zhongshan Cuiheng National Wetland Park, and other natural protection areas adjust their water levels to create diverse depths, catering to the foraging requirements of different bird species. Additionally, management agencies employ extensive approaches to minimize human interference, such as prohibiting pesticide and fertilizer application, and promoting the growth of reeds and aquatic grasses, which offer shelter for birds. Similar initiatives in places, such as the Mai Po Nature Reserve in Hong Kong, have successfully enhanced waterbird abundance through artificial aquaculture pond management (Wei et al., 2017).

5 Conclusion

Natural protected areas play a crucial role in upholding bird diversity amid high-intensity human activities, forming an integral part of biodiversity conservation strategies. Our findings revealed notable variations in how different bird types respond to common environmental drivers. Specifically, the extent of aquaculture pond area, mangrove coverage, and mudflat area emerged as pivotal factors influencing bird diversity, with interpretation rates of 31.0%, 28.9%, and 20.3%, respectively. Mangrove coverage significantly influenced the diversity of songbirds, climbing birds, raptors, terrestrial birds, and others, whereas the area of aquaculture ponds notably affected wading and swimming birds. Although birds exhibited relatively subdued responses to water and soil environments, the significance of these factors in shaping their diversity cannot be ignored. Further investigations is warranted to elucidate the precise impact of these drivers on bird diversity. Although other environmental factors, such as COD, nitrate concentration, and salinity, were less significant drivers of bird diversity compared to aquaculture pond area, mangrove coverage, and mudflat area, they still had an impact. Investigating how these factors affect bird diversity is a worthwhile topic for future studies.

The Chinese government aims to expand mangrove planting within protected natural areas under the *Specific Project for the Protection and Restoration of Mangroves* (2020–2025). To enhance the protection of mangrove bird diversity, management authorities

should judiciously oversee mangroves, mudflat, and aquaculture pond areas while formulating mangrove forest protection and restoration plans. This approach ensures that large-scale mangrove planting does not encroach upon the habitats of non-mangrove species. Furthermore, scientific management of aquaculture ponds, including water level regulation, is essential to meet diverse bird habitat requirements.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding authors.

Author contributions

XY: Writing – original draft, Writing – review & editing, Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization. RW: Methodology, Software, Writing – review & editing, Conceptualization. CZ: Data curation, Writing – original draft. MQ: Formal analysis, Writing – original draft. JL: Data curation, Writing – original draft. RY: Data curation, Writing – review & editing. YZ: Methodology, Writing – original draft. GH: Resources, Writing – original draft. KT: Methodology, Writing – review & editing. LY: Methodology, Writing – original draft. SY: Writing – review & editing.

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Author SY was employed by the company Guangzhou Yuanheng Natural Resources Technology Co., Ltd.

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