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Density and spatial distribution of migratory shorebirds in different foraging habitats in the coastal region of Piauí State, Brazil

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ABSTRACT

Coastal habitats are important feeding grounds for migratory shorebirds, which turns the coast of Piauí State into an important region for birds' migration cycle. This study aimed to identify migratory shorebirds, analyze their patterns of habitat preference on coastal Piauí State, Brazil, and identify classes of invertebrates found in foraging sites. In total, 23,829 records of migratory shorebirds belonging to 15 species were found at feeding sites, presenting significant segregation between different foraging substrates ($F_{1,23} = 8.41$; $p = 0.001$). *Limnodromus griseus* (56.5±98.42; $p > 0.001$), *Numenius hudsonicus* (35.96±37.37; $p > 0.001$), and *Calidris canutus* (34.4±80.84; $p < 0.001$) were the species accounting for the highest densities in muddy substrate. *Calidris pusilla* (77.37±178.02; $p > 0.001$), *Charadrius semipalmatus* (66±142.17: $p > 0.001$), and *Calidris alba* (56.5±181.24; $p > 0.001$) were the most significant species in sandy-muddy substrate. Birds' lowest density was observed in sandy habitat, but *C. alba* (22.41±40.9) recorded the highest density in this substrate. Overall, most shorebirds (92.8 %) preferred foraging substrates presenting higher concentration of fine particles (silt, clay, and fine sand). Invertebrates belonging to classes Polychaeta, Gastropoda, Bivalvia, and Malacostraca prevailed in these sites. Therefore, substrate type and prey composition are factors influencing the density of migratory shorebirds in foraging sites. In addition, this region witnesses the occurrence of endangered species, and it reinforces the importance of these feeding sites for them during their migration to Brazil's coastal region.

Keywords: Birds, Charadriiformes, Aquatic invertebrates, Feeding site, Coastal zonest

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INTRODUCTION

Shorebirds' (order Charadriiformes) classification is linked to their habit of feeding on small invertebrates who live in humid habitats (Iglesia and Winn, 2021). Approximately 80% of shorebird species living in the Americas perform some sort of seasonal movement between non-breeding and breeding sites, and it can involve different continents (Iglecia and Winn, 2021). Thus, several species reproduce in breeding regions, such as the Arctic and Alaska, then migrate to the Southern Hemisphere, where they find sites presenting rich diversity of invertebrates, mainly mollusks, arthropods, and annelids. These invertebrates play important role as dietary resources for these birds' survival (Lunardi et al., 2012; Fedrizzi et al., 2016).

Wetlands in South America's coastal regions, such as estuaries and rivers, stand out among the most important sites for shorebirds' migration cycle, mainly intertidal zones (Lunardi et al., 2012; Silva and Rodrigues, 2015). According to Paludo et al. (2022), 56 strategic sites in Brazil are officially acknowledged as conservation sites for shorebirds given the high density of these birds in these regions. In total, 43 of these sites are found in the Coastal Zone. These habitats are featured by different sedimentary compositions (sand, silt, clay, and organic matter) that, in turn, can influence the distribution of marine invertebrates (Neves and Bemvenuti, 2009; Baroni and Borges, 2015; Souza et al., 2020).

Knowledge about migratory shorebirds' feeding sites and preferred feeding habitats can be an important tool for species conservation purposes (Paludo et al., 2022). Thus, this study aimed to analyze foraging habitat use patterns adopted by migratory shorebirds in three substrate types (muddy, sandy-muddy, and sandy) in Piauí State's coastal region, Brazil.

METHODS

Study site

The coast of Piauí State is 66 km long and accounts for approximately 0.89% of the Brazilian coast. It is located between geographic coordinates 2°42'35" and 3°05'02" South and 41°14'53" and 41°52'46" West, and borders Maranhão State to the West and Ceará State to the East. This study was focused on four different sites, namely: Parnaíba River estuary (A1; 2°44'56.59"S, 41°47'4.03"O), Igaraçu River estuary (A2; 2°51'36.05"S, 41°38'58.87"O), the estuaries of Cardoso and Camurupim rivers (A3; 2°54'50.36"S, 41°26'21.10"O), and the estuaries of Timonha and Ubatuba rivers (A4; 2°55'51.71"S, 41°18'49.33"O) (Figure 1). These sites suffer from human activities such as fishing, shrimp farming, energy generation (wind farms), and sun and beach tourism (Braga et al., 2022; Meireles and Campos, 2011). The study site is part of Delta do Parnaíba Environmental Protection Area (EPA).

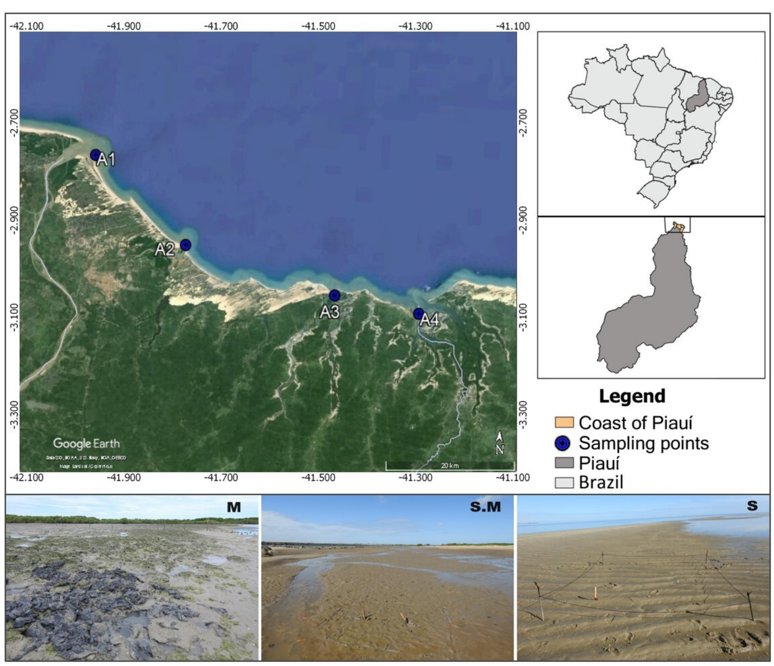

Figure 1. Piauí State's coast, Brazil. Caption: A1: Parnaíba River; A2: Igaraçu River; A3: Cardoso and Camurupim rivers; A4: Timonha and Ubatuba rivers. M: muddy; S.M: sandy-muddy; S: sandy.

The morphology of Piauí State's coastal region is mainly featured by dunes, marshes, marine erosions with granite outcrops, sandy and clayey sedimentation with sandstone incidence, and the prevalence of *restinga* vegetation (Baptista, 1981; Araújo et al., 2019). Climate in this region is defined by a rainy period (from January to June), which registers annual rainfall rate close to 150 mm, as well as by a dry period (from July to December) featured by low rainfall rates. Moreover, it is featured by strong winds, whose speed can range from 1.3 m s^{-1} to 7 m s^{-1}, according to Ferreira and Kemenes (2023).

Shorebirds

Bird censuses were conducted every month along the intertidal zone from May 2021 to April 2022, following the linear transect methodology (Vielliard et al., 2010) (Figure 2). In total, three transects (1 km each) were selected for each site. They were classified as T1, T2, T3 (distributed at A1), T4, T5, T6 (distributed at A2), T7, T8, T9 (distributed at A3), T10, T11, and T12 (distributed at A4). Then, these transects were classified into muddy, sandy-muddy, and sandy substrates based on soil granulometric features. Sampling was conducted during the low tide and it considered the period presenting the highest shorebird concentration on feeding banks. Each substrate was sampled for one hour, and it totaled 144 hours of observation (1 hour × 3 substrate types × 4 areas × 12 months). Binoculars, spyglasses, digital cameras, and field guides were used to record the birds (Sigrist, 2009; Hayman et al., 2010; Sigrist, 2014).

Figure 2. Transects distribution (Muddy, Sandy-muddy, and Sandy) in the sampling areas: A1: Parnaíba River; A2: Igaraçu River; A3: Cardoso and Camurupim rivers; A4: Timonha and Ubatuba rivers.

Macroinvertebrates

Sampling procedures were conducted in 2 m² quadrants that were randomly distributed in each substrate type, from January to April 2022 (adapted from Lunardi et al., 2012), at the times of greatest bird abundance in the region. This aimed to investigate the density of macroinvertebrates (potential preys) in different substrates. Samples were collected with a 0.5-mm sieve, from soil layer 0–20 cm. Collected specimens were taken to laboratories and identified up to Class taxonomic level.

Granulometry

From January to April 2022, 12 soil samples were collected—one from each substrate type (muddy, sandy-muddy, and sandy)—to feature the granulometry prevailing in each foraging site. Then, they were dried in oven at 80°C until the sediment was fully dry. After this procedure was over, different particle sizes were selected with sieves (diameters ranging from 2 mm to 0.053 mm) and classified into coarse (particle size ranging from 2 mm to 1.18 mm), medium (particle size ranging from 0.5 mm to 0.25 mm), and fine sand (particle size equal to 0.15 mm), as well as silts + clay (particle size equal to or smaller than 0.053 mm) (adapted from Lunardi et al., 2012). Transects presenting silt and clay concentrations higher than 50% of particles found in the analyzed samples were classified as muddy habitat, whereas transects in which the sum of coarse and medium sand was higher than 50% of the aforementioned particles were classified as muddy habitat. The other transects, which did not meet the previous criteria and presented higher particle concentration homogeneity were classified as sandy-muddy substrate.

Statistical analysis

The abundance of each migratory shorebird species was associated with foraging habitat by considering habitat type classification based on both granulometric composition and particle size (Sandy, Muddy, and Sandy-Muddy). This aimed to analyze the habitat preference of these species along all four monitored sites at Piauí State's coastal region. These habitat-type variables were initially assessed for their collinearity level via Variance Inflation Factor (VIF), in which VIF values ≤ 7 were used as cut-off point. Moreover, Pearson's correlation coefficient was adopted to assess their correlation level. These procedures found no collinear or correlated variables. However, in case collinear or correlated variables were identified, one of them would be excluded from the analysis to avoid likely statistical bias. All these procedures were conducted following the recommendations by Zuur et al. (2010).

The vegan package (Oksanen et al., 2020) was used in bird abundance data matrix to estimate the dissimilarity index of different foraging habitat types via the Bray–Curtis method (Bray and Curtis, 1957). The aforementioned matrix only considered records from September to May, when the highest shorebird incidence can be observed in Brazil (Iglecia and Winn, 2021). Canonical correspondence analysis (CCA) was performed to correlate the abundance distribution of migratory shorebird species observed in this study that used different foraging habitat types, being conducted after the dissimilarity matrix was created (Ter Braak, 1995). Permutation Multivariate Analysis of Variance (PERMANOVA) was used to assess significance level (Anderson, 2005). Moreover, Wilcoxon test was applied to each observed species to identify likely differences in abundance between different foraging habitats.

RESULTS

Granulometry

Transects T4, T7, T10, and T11 presented high silt and clay composition. Thus, they were classified as muddy habitat (M). Transects T3, T6, T9, and T12 were classified as sandy habitat (S) due to their high coarse and medium sand concentration. Finally, transects T1, T2, T5, and T8 were featured as sandy-muddy (S.M) (Table 1). The finest sedimentation in the muddy and sandy-muddy transects may have resulted from these sites' location, as their distribution is closely associated with the lower intertidal zone line where they suffer little impact from waves. It differs from the sandy transects distributed in the middle band of the intertidal zone, where there is greater influence of waves and marine currents.

Table 1. Particle concentrations (%) of substrates found in the different analyzed transects. Caption: T1–12: Transects distributed in four sampling sites based on birds' feeding habitat.

Transects	Coarse sand (2 mm to 1.18 mm)	Medium sand (0.5 mm to 0. 25 mm)	Fine sand (0.15 mm)	Silt and Clay (= or < 0.053 mm)
T1	5.6	18.32	30.9	45.2
T2	0.8	11.13	47.61	40.47
T3	6	51.03	38.19	4.5
T4	3.38	14.36	18.91	63.37
T5	1.77	19.66	49.48	29.1
T6	19.68	64.58	12.46	3.3
T7	11.49	16.09	12.05	60.39
T8	5.35	14.28	30.26	46.13
T9	6.16	74.86	10.29	8.71
T10	9.66	15.18	6.02	69.17
T11	6.62	6.99	3.41	83
T12	23.98	69.47	3.86	2.71

Macroinvertebrates

In total, 713 contacts with invertebrate specimens belonging to phyla Annelida, Mollusca, and Arthropoda were recorded. Abundance analysis conducted via Chi-squared test showed that the sandy-muddy habitat is more abundant than the muddy (X2 (5) = 133.8; $p < 0.001$) and sandy (X2 (5) = 93.2; $p < 0.001$) ones. The muddy habitat presented prevalence of invertebrates belonging to Classes Polychaeta, Gastropoda, and Bivalvia, which recorded 59%, 17.5%, and 11.7% relative abundance, respectively. On the other hand, the sandy-muddy habitat presented prevalence of Classes Bivalvia, Polychaeta, and Malacostraca (Brachyura, Caridea, Dendrobranchiata, Anthuridea, and Anomura), which recorded 47.8%, 27%, and 14.9% relative abundance, respectively. The sandy habitat, in its turn, presented prevalence of Classes Bivalvia and Gastropoda, which recorded 63% and 30.3% relative abundance, respectively (Table 2).

Table 2. Relative abundance of invertebrate classes recorded in different shorebird's feeding substrates in Piauí State's coast, Brazil. Caption: RA%: relative abundance. No. Total number of invertebrates.

Substrate	RA%			No.
Taxon	Muddy	Sandy-Muddy	Sandy	
Phylum Annelida				
Class Polychaeta	59	27	0.6	252
Phylum Mollusca				
Class Bivalvia	11.7	47.8	63	282
Class Gastropoda	17.5	7.8	30.3	119
Phylum Arthropoda				
Class Malacostraca	6	14.9	4.1	
Order Decapoda				
Infraorder Anomura				19
Infraorder Brachyura				13
Infraorder Caridea				2
Suborder Dendrobranchiata				4
Order Isopoda				
Suborder Anthuridea				
Class Maxillopoda	5.7	0	0	
Subclass Cirripedia				15
Class Insecta	0	2.5	1.8	
Order Coleoptera				7

Shorebirds

In total, 23,829 records of 15 migratory shorebird species belonging to families Scolopacidae and Charadriidae were made (Table 3). However, *Calidris fuscicollis* (White-rumped Sandpiper) was removed from the analysis since it recorded a significantly smaller number of individuals in the investigated sites. The highest bird abundance rate was observed in the sandy-muddy substrate, which recorded 11,709 individuals, being followed by the muddy substrate (10,409 individuals). The sandy substrate recorded 1,711 individuals. *Calidris pusilla* (Semipalmated Sandpiper; n = 7,122 records), *Charadrius semipalmatus* (Semipalmated Plover; n = 3,671 records), and *Limnodromus griseus* (Short-billed Dowitcher; n = 3,267 records) were the most abundant species in it, whereas *Tringa melanoleuca* (Greater Yellowlegs; n = 35 records), *Pluvialis dominica* (American Golden-Plover; n = 8 records), and White-rumped Sandpiper (n = 2 records) recorded the lowest abundance rates in the investigated region (Table 4).

Table 3. Migratory shorebirds recorded in the investigated sites. Caption: CR: critically endangered; EN: endangered; LC: of little concern.

Taxon	ICMBio	Common name in Brazilian Portuguese	Common name in English
Charadriiformes Huxley, 1867			
Charadriidae Leach, 1820			
Charadrius semipalmatus	LC	*batuíra-de-bando*	Semipalmated Plover
Pluvialis squatarola	LC	*batuiruçu-de-axila-preta*	Black-bellied Plover
Pluvialis dominica	LC	*batuiruçu*	American Golden-Plover
Scolopacidae Rafinesque, 1815			
Arenaria interpres	LC	*vira-pedras*	Ruddy Turnstone
Actitis macularius	LC	*maçarico-pintado*	Spotted sandpiper
Calidris alba	LC	*maçarico-branco*	Sanderling
Calidris minutilla	LC	*maçariquinho*	Least Sandpiper
Calidris pusilla	EN	*maçarico-rasteirinho*	Semipalmated Sandpiper
Calidris canutus	CR	*maçarico-de-papo-vermelho*	Red Knot
Limnodromus griseus	CR	*maçarico-de-costas-brancas*	Short-billed Dowitcher
Numenius hudsonicus	LC	*maçarico-de-bico-torto*	Hudsonian Whimbrel
Tringa flavipes	LC	*maçarico-de-perna-amarela*	Lesser Yellowlegs
Tringa melanoleuca	LC	*maçarico-grande-de-perna-amarela*	Greater Yellowlegs
Tringa semipalmata	LC	*maçarico-de-asa-branca*	Eastern Willet
Calidris fuscicollis	LC	*maçarico-de-sobre-branco*	White-rumped sandpiper

As for the composition and abundance of migratory shorebirds in feeding sites, there was significant segregation of migratory shorebird communities among the analyzed forage substrates ($F_{1,23}$ = 8.41 p = 0.001; Figure 3). This finding points towards certain preference by some groups of birds for specific substrate types. Short-billed Dowitcher (56.5±98.42; p > 0.001), *Numenius hudsonicus* (Hudsonian Whimbrel; 35.96±37.37; p > 0.001), and *Calidris canutus* (Red Knot; 34.4±80.84; p < 0.001) were the bird species showing the most significant numbers of records in the muddy substrate. Semipalmated Sandpiper (77.37±178.02; p > 0.001), Semipalmated Plover (66±142.17: p > 0.001), *Calidris alba* (Sanderling; 56.5±181.24; p > 0.001), *Arenaria interpres* (Ruddy Turnstone; 33.37±77.18; p = 0.002), and *L. griseus* (29.93±74.57; p = 0.01) were the most significant species in the sandy-muddy substrate. The sandy habitat was the one presenting the smallest number of bird records (Table 2). Sanderling (22.41±40.9; p = 0.16) and *Pluvialis squatarola* (Black-bellied Plover; 10.28±23.78; p = 0.15) were the only species recording high relative frequency rates in these habitats (Table 4; Table 5).

Table 4. Concentration of migratory shorebird on different substrates. Caption: RA%: relative abundance; M: mean; SD: standard deviation; NA: not analyzed due to species' low incidence.

Taxon	M ± SD (RA%)		
	Muddy	Sandy-muddy	Sandy
Charadrius semipalmatus	16.34±15.44 (6.96)	66±142.17 (21)	3.78±9.68 (0.7)
Pluvialis squatarola	21.15±36.38 (8)	27.37±58.07 (7.7)	10.28±23.78 (20.5)
Pluvialis dominica	0.03±0.17 (0.01)	0.18±0.78 (0.05)	0±0 (0)
Arenaria interpres	19.81±18.82 (7.3)	33.37±77.18 (9.7)	4.87±6.74 (9.3)
Actitis macularius	7.17±9.12 (2)	0.54±1.1 (0.13)	0±0 (0)
Calidris alba	0.42±2.26 (0.1)	56.5±181.24 (16.6)	22.41±40.9 (43.7)
Calidris minutilla	3.53±5.28 (1.0)	1.09±2.34 (0.6)	0±0 (0)
Calidris pusilla	69.87±114.26 (26)	77.37±178.02 (31)	4.15±9.77 (8.3)
Calidris canutus	34.4±80.84 (11.8)	3.09±7.32 (0.8)	0.18±0.89 (0.46)
Limnodromus griseus	56.5±98.42 (19.3)	29.93±74.57 (9.5)	3.93±14.74 (0.7)
Numenius hudsonicus	35.96±37.37 (13)	4.46±5.9 (1.6)	0.53±1.72 (0.1)
Tringa flavipes	2.25±7.31 (0.7)	2±5.25 (0.5)	0.65±2.71 (1.3)
Tringa melanoleuca	0.53±1.24 (0.2)	0.12±0.55 (0.07)	0.21±0.65 (0.46)
Tringa semipalmata	7.52±15.64 (3.4)	1.41±5.57 (0.03)	0±0 (0)
Calidris fuscicollis	NA	NA	NA

Table 5. P-values obtained from modeling of species in the three types of substrates. Caption: NA: not analyzed due to the species' low occurrence. P-values: * indicate significant values.

Species	Sandy × Sandy-muddy	Sandy × muddy	Sandy-muddy × muddy
Pluvialis dominica	0.48	0.5	0.55
Pluvialis squatarola	0.15	0.31	0.67
Charadrius semipalmatus	>0.001*	>0.001*	0.6
Limnodromus griseus	0.05	>0.001*	0.01*
Numenius hudsonicus	>0.001*	>0.001*	>0.001*
Actitis macularius	0.01*	>0.001*	>0.001*
Calidris alba	0.16	>0.001*	>0.001*
Calidris fuscicollis	NA	NA	NA
Calidris minutilla	0.008*	0.04*	>0.001*
Calidris pusilla	0.06	>0.001	0.06
Calidris canutus	0.06*	0.001*	0.06
Arenaria interpres	0.13	0.002*	0.13
Tringa flavipes	0.28	0.08	0.37
Tringa melanoleuca	0.41	0.31	0.13
Tringa semipalmata	>0.001*	>0.001*	0.09

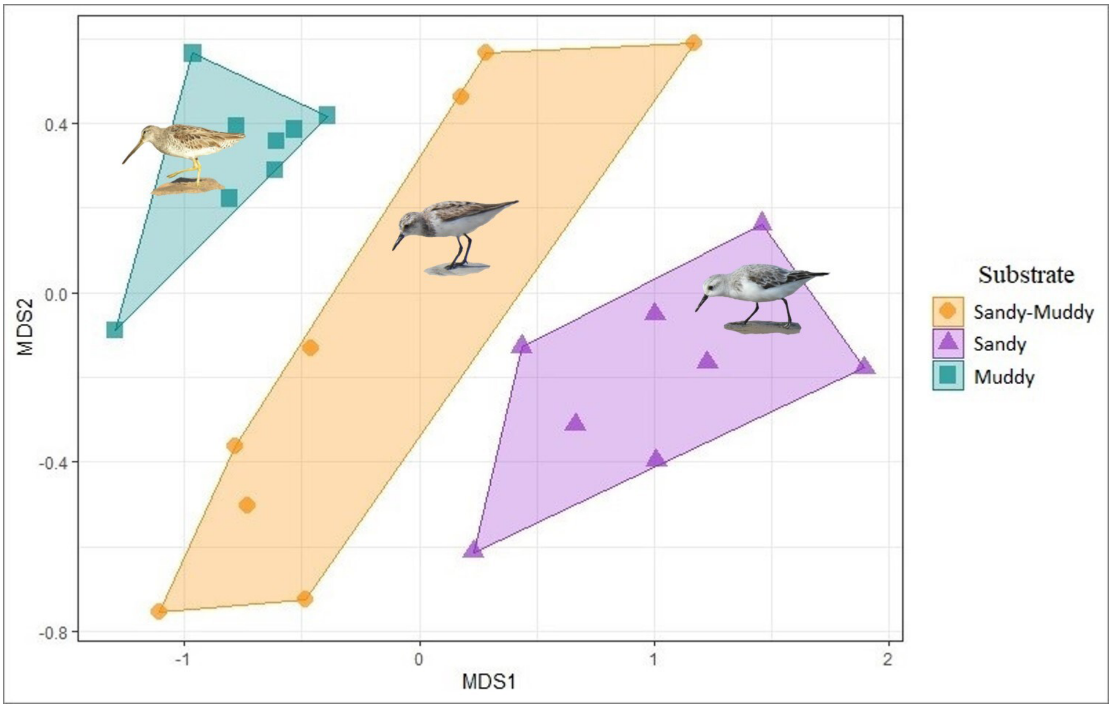

Figure 3. Non-metric multidimensional scaling (NMDS) of migratory shorebirds recorded in three foraging substrates at Piauí State's coast, Brazil.

DISCUSSION

The highest density rates recorded for migratory shorebirds in feeding habitats located in the coast of Piauí State were observed in sandy-muddy and muddy substrates. These substrates also recorded the highest potential prey densities, mainly for invertebrates belonging to Classes Polychaeta, Bivalvia, Gastropoda, and Malacostraca. The distribution of invertebrates in different foraging habitats can be closely linked to substrate size and composition since these elements can affect food availability for benthic invertebrates (Choi et al., 2014). These invertebrates work as important organic matter cycle regulators in the food chain (Saint-Béat et al., 2013). Intertidal habitats often present higher organic matter concentrations, so they tend to host large numbers of invertebrates belonging to Class Polychaeta. These invertebrates, in turn, are one of the main food sources for migratory shorebirds (Silva and Rodrigues, 2015; Santos et al., 2019).

Unlike muddy and sandy-muddy habitats where clay and silt presence helps fixing sediment and organic matter, sandy habitats suffer from higher hydrodynamic impact. Thus, loose particles are more susceptible to be removed from them by currents. Therefore, it affects organic matter fixation in environments presenting low richness of marine invertebrates (Vanden Eede et al., 2014) and, consequently, lower food availability for shorebirds (Silva and Rodrigues, 2015). Moreover, sandy habitats also suffer significant human interference due to foot traffic, for example. This interference can significantly change both the composition and density of invertebrates living in them due to "trampling" pressure on these sites (Schlacher et al., 2016). Notably, sandy transects suffer from greater people flow and vehicles' circulation because of activities mainly linked to tourism. These activities are considered potential threats to these sites and can cause disturbances and scare birds away from these substrates (Burger et al., 2004; Schlacher et al., 2013).

The highest migratory shorebird densities recorded in this study were observed in substrates presenting higher diversity and abundance of invertebrates. This finding supports the hypothesis that birds' preference for foraging on specific substrates is associated with the higher biomass of invertebrates concentrated in these places, as suggested by Smith et al. (2012). From this perspective, the current results corroborate other studies, according to which the highest shorebird concentrations were observed in the thinnest substrates presenting the highest prey density (Lunardi et al., 2012; Silva and Rodrigues, 2015). Polychaetes are one of the main food items consumed by shorebirds and they prevail in environments with high organic matter content. They are often found in these places (Fonseca and Navedo, 2020), as observed in the herein investigated muddy and sandy-muddy habitats. The consumption of soft-bodied preys, available in foraging habitats, such as polychaetes, may be more advantageous for shorebirds since they can save both time and energy in their digestive process (Van Gils et al., 2003; Ersoy et al., 2022).

Calidris pusilla (Figure 4A), which is classified as nationally endangered species (ICMBio, 2018), was the most abundant shorebird in this study. The highest abundance of it was observed in sandy-muddy and muddy habitats. This finding corroborates the highest density of Malacostracas, Bivalvia, and Polychaeta—which are three of the main groups of invertebrates consumed by *C. pusilla*—in these environments (Beauchamp, 2009; Churchwell et al., 2018; Santos et al., 2019; Linhart et al., 2022). Although the diversity of preys in the diet of shorebirds may change, the higher concentration of polychaetes found in thinner substrates may have been a determining factor for the higher *C. pusilla* concentration in sandy-muddy and muddy habitats, as observed in other studies (Santos et al., 2019). Similar results were also reported by Silva and Rodrigues (2015), according to whom, the aforementioned species was more abundant in the muddy habitat, which also recorded the highest density of polychaetes.

Limnodromus griseus (Figure 4B), which is nationally endangered (ICMBio, 2018) and recorded significant abundance in this study, also recorded higher density in the muddy habitat. This finding corroborates results reported by Silva and Rodrigues (2015). According to fecal analyses conducted in other studies, polychaetes are the main invertebrates consumed by species *L. griseus* (Fedrizzi et al., 2016). This finding may explain the highest densities observed for this species in substrates dominated by them. Moreover, *L. griseus* shows preference for foraging in more humid and submerged habitats, where its representatives' long beak can penetrate the soft mud to capture invertebrates in the substrate (Robert and Mcneil, 1989; Kober and Bairlein, 2009).

Calidris canutus (Figure 4C), which is another endangered species in Brazil (ICMBio, 2018), was found in all investigated substrate types. However, its highest density was recorded in muddy and sandy-muddy habitats. This finding corroborated other studies, such as that by Silva and Rodrigues (2015). *C. canutus* tends to select habitats with high prey abundance, and it is a strategy to maximize prey consumption within a short period-of-time (Heller et al., 2022). Polychaetes, mollusks (mainly bivalves), and crustaceans are often among preys mostly consumed by this species (Dekinga and Piersma, 1993; Van Gils and Piersma, 2004; Hernández et al., 2008; Fedrizzi et al., 2016). According to studies available in the literature, bivalves belonging to families Mactridae and Donacidae (which are abundant in the sandy-muddy habitat) are the main food source among mollusks consumed by *C. canutus* in some places (Hernández et al., 2008; Cohen et al., 2010; Fedrizzi et al., 2016). However, whenever resources are available, *C. canutus* can change its consumption rate between soft-bodied and hard-bodied preys. This behavior requires different digestion efforts. It means that the consumption of polychaetes can be advantageous in environments where *C. canutus* finds greater variety of prey. This can be explained by the fact that digesting polychaetes requires shorter time and lower energy spending (Van Gils et al., 2003; Van Gils and Piersma, 2004; Ersoy et al., 2022).

Calidris alba (Figure 4D) mainly breeds in the Arctic. After that, it migrates to other non-breeding areas. Its migration through the Americas takes place mainly along the Atlantic route, from the Arctic to the entire Brazilian coast (Lyra-Neves et al., 2004; Delchiaro et al., 2013). Its representatives can feed in sandy habitats due to tactile-continuous hunting strategies, such as pecking and probing, although it can change between beaches and lagoons (Silva and Rodrigues, 2015; Angarita-Báez and Carlos, 2024). The highest *C. alba* density in sandy-substrate habitats can be a response to the high concentration of bivalves in these habitats, as these invertebrates are among the main prey consumed by the species (Nuka et al., 2005; Grond et al., 2015). However, the low density of bivalves can force the species to feed on other resources available in the feeding site, such as annelids, crustaceans, and insects (Grond et al., 2015; Angarita-Báez and Carlos, 2024). Delaware Bay, USA, where the species mainly feeds on horseshoe crab eggs (Limulus polyphemus), is an important stopover site for this species during spring migration (Castro et al., 1989).

Figure 4. Migratory shorebirds recorded in the investigated sites. A: *C. pusilla*: B: *L. griseus*; C: *C. canutus*; D: *C. alba*.

Species belonging to genus *Numenius* often feed on crab in coastal regions (Backwell et al., 1998; Fedrizzi et al., 2016; Morales-Torres et al., 2024). However, the incidence of these crustaceans in the herein analyzed substrates was significantly low. This finding points towards *N. hudsonicus* feeding on invertebrates that are more abundant in this substrate, such as gastropods, bivalves, and annelids, as well as on groups of invertebrates already found in fecal analyses of this species' representatives (Fedrizzi et al., 2016). Notably, *N. hudsonicus* has been spotted foraging in mangrove areas, and this ecosystem can house larger populations of crustaceans (Aveline, 1980). However, the direct distribution of invertebrates in this ecosystem was not assessed in the present research.

Although the herein identified invertebrate groups were assumed as the main food sources available for migratory shorebirds in Delta do Parnaíba Environmental Protection Area, we emphasize that shorebirds can present generalist or opportunistic behaviors. In other words, they are able to use other food sources available in certain regions, such as invertebrates (Coleoptera, Lepidoptera, Hymenoptera, Arachnids and

Hemiptera), vegetables, and even fish (Smith et al., 2012; Faria et al., 2018). Therefore, migratory shorebirds can flex their trophic responses to maximize prey intake depending on the availability of resources in a given feeding site (Gonzales et al., 2022). Moreover, shorebirds can compensate and maximize their prey intake at night, when the availability of resources can be higher and birds face fewer threats (Robert and Mcneil, 1989; Mcneil and Rodriguez, 1996). According to Esser et al. (2008), prey abundance does not significantly change between daylight and nighttime. However, some invertebrates, such as polychaetes, show significantly higher abundance on ground surface at night. This finding suggests that this prey can be largely available to shorebirds at night.

CONCLUSION

This study shows that prey composition and substrate type are factors strongly contributing to the composition and abundance of migratory shorebirds in tropical foraging sites. Although most shorebirds prefer muddy habitats presenting higher concentration of polychaetes, other birds, such as *C. alba,* preferred sandy foraging sites presenting a larger number of bivalves. Yet, based on the present results, this area is essential for the occurrence of nationally endangered migratory shorebirds, such as *C. canutus*, *C. pusilla*, and *L. griseus.* This finding reinforces the relevance of conserving feeding areas for migratory shorebirds at Delta do Parnaíba Environmental Protection Area (APADP), coastal zone of Piauí State, Brazil. Accordingly, these results subsidize actions to limit human activities in order to preserve these species' feeding sites in future revisions of the APADP management plan.

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AUTHOR CONTRIBUTIONS

A.J.S.S.: Concept; Methodology; Investigation; Formal Analysis; Writing - Original draft; WritingReview & Editing.

M.S.N.: Investigation; Writing: Review & Editing.

J.P.D.: Data Curation; Methodology; Software; Formal Analysis; Investigation; Writing – Review & Editing.

J.M.G.; B.L.G.; F.J.P.F: Formal Analysis; Investigation; Writing – Review & Editing.

A.G.: Supervision; Resources; Project Management; Funding acquisition; Writing – Review & editing.

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