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Sea-level rise causes feeding habitat loss for migratory shorebirds in remote coastal wetlands of Brazilian Amazon

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Abstract

Sea-level rise (SLR) can cause significant changes in coastal wetlands, such as the retreat of coastlines and sedimentary shifts in tidal flats. In areas lacking coastal defenses, rising sea levels are expected to drive the inland migration of coastal wetlands, generally maintaining the extent of tidal flat habitats but also triggering important ecosystem changes. Migratory shorebirds are apex predators in coastal wetlands, thus being highly sensitive to such changes. Despite the worldwide decline of this group of birds, the impacts of SLR on their habitats have not been readily evaluated. In this study, we investigated how migratory shorebirds are responding to the gradual occupation of tidal flats by areas originating from marine transgression of terrestrial habitats, which is a consequence of inland migration of coastal wetlands. We conducted aerial surveys to assess the distribution of shorebirds along 630 km of tidal flats in coastal wetlands of the Brazilian Amazon. We then mapped the distribution of tidal flats in the late 1980s and for the survey period using satellite imagery to identify the tidal areas created by marine transgression over the past four decades. Finally, we sampled these areas and nearby tidal flats to assess shorebird prey abundance and sediment characteristics. We found that shorebirds avoid transgressed areas as feeding grounds, with their numbers sharply declining with the increasing occupancy of this habitat. The dominant shorebird species, the semipalmated sandpiper (*Calidris pusilla*), presented densities one order of magnitude lower in transgressed areas than in other tidal flats, indicating a clear response to the reduced availability of its main prey, the crustacean *Discapseudes surinamensis*. We conclude that, although inland migration of coastal wetlands may preserve the extent of tidal flats over time, their increased occupation by transgressed areas can lead to significant losses in feeding habitat for migratory shorebirds.

1. Introduction

Sea-level rise (SLR) is one of the most prominent and profound repercussions of global warming. This phenomenon primarily results from the melting of polar ice sheets and the thermal expansion of seawater due to increasing temperature [1]. Over the last three decades, the global sea level has been rising at an average rate of 3.3 mm per year, also showing clear signs of acceleration [2]. The Intergovernmental Panel on Climate Change (IPCC) projected that global sea level will rise between 0.53 and 1.75 m by 2100 [3].

SLR can have significant impacts on coastal wetlands. As water depth increases, stronger tidal currents and wave action tend to reshape the coastline through erosion, leading to its retreat while also creating steeper shorelines with coarser tidal sediments [4–6]. In lower lying areas, SLR may also cause coastal flooding and saltwater intrusion into groundwater and freshwater of adjacent wetlands [6, 7]. These changes are usually reflected at the ecosystem level, with organisms readapting their distributions to cope with the new environmental conditions [8, 9]. As apex predators in coastal wetlands, shorebirds are highly sensitive environmental stressors propagated throughout the ecosystem and are expected to respond to the effects of SLR through changes in population size, distribution and behavior [10].

More than half of all migratory shorebird species worldwide are currently declining [11]. These birds typically breed at high latitudes of the northern hemisphere and spend their non-breeding season in coastal wetlands of temperate and tropical regions [12]. While direct human pressures on coastal wetlands such as land reclamation, pollution, shellfishing, and hunting are known factors contributing to shorebird declines [13, 14], there is still limited evidence regarding how these birds may be affected by the environmental changes induced by SLR (but see [15–18]). In coastal wetlands where coastlines are protected by artificial defenses (e.g. dikes and seawalls), the gradual squeezing of tidal habitats is expected to exacerbate erosion, impacting shorebirds through the reduction of prey abundance and exposure period of tidal flats [5, 15, 19]. However, many non-breeding areas of migratory shorebirds are located in remote areas with little or no human intervention, particularly in tropical and subtropical regions [12]. In these locations, tidal habitats are expected to respond to SLR through a gradual inland migration [6, 20]. While the seaside edges of tidal flats are prone to erosion due to the increase in tidal currents, marine transgression during spring high tides and storm surges is expected to convert nearshore terrestrial habitats into new tidal flats [6, 20, 21]. According to this dynamic, it may be predicted that tidal flats in remote wetlands tend to conserve their overall extension over time, even under the influence of SLR [6, 21]. This prediction has been validated by recent studies [22, 23]. However, despite potential compensation for losses by newly formed tidal flats resulting from transgression, the value of these new habitats as feeding grounds for migratory shorebirds has not yet been quantified. Such information is critical for understanding how this group of birds is coping with SLR and adopting the necessary conservation actions.

The coast of the Brazilian Amazon stands among the most important non-breeding grounds for migratory shorebirds in the Atlantic Americas Flyway, having been estimated to host ca. 360 000 individuals across the different species [24]. This region comprises extensive pristine coastal wetlands with vast extensions of tidal flats bordered by the largest continuous mangrove forest in the world [25, 26]. Despite being largely unpopulated, this region is highly vulnerable to SLR due to the low elevation of coastal areas, combined with the effects of macrotides and tropical storms [25, 27]. Recent studies have reported large-scale saltwater intrusion in this region, documented by an accelerated inland migration of mangroves and the salinization of freshwater lakes [9, 28]. Low altitude aerial surveys conducted in recent years further suggested that large sections of tidal areas have originated from marine transgression, evidenced by the presence of ghost mangrove forests and abundant trunks lying over the tidal flats (authors' pers. obs.). Taken together, the exacerbated effects of SLR and the great abundance of migratory shorebirds in this region provide a unique opportunity to investigate how these birds are adapting to the effects of SLR, which are expected to intensify in coastal wetlands around the world in coming decades.

This study aims to quantify the relative importance of tidal flats resulting from marine transgression as feeding grounds for migratory shorebirds, given the growing relevance of this habitat in coastal wetlands as SLR progresses. To achieve this goal, we conducted aerial surveys in 2018 and 2020 to assess the distribution of migratory shorebirds along 630 km of coastline covered by tidal flats in the State of Amapá (Brazil). We then mapped the distribution of tidal flats in this area during the late 1980s and for the aerial survey period using satellite imagery. The overlapping of these maps allowed us to distinguish between tidal flats resulting from marine transgression since the late 1980s (hereafter referred to as 'transgressed areas') from other tidal flats. Finally, we modeled the influence of tidal flat origin on their utilization by migratory shorebirds. Considering the distinct characteristics of sediments in transgressed areas, we hypothesized that these tidal habitats present differentiated communities of benthic macroinvertebrates prompting foraging adjustments by migratory shorebirds.

2. Material and methods

2.1. Study area

The study area encompasses ca. 630 km of coastline in the state of Amapá (Brazil), lying within the equatorial region of northern South America (figure 1).

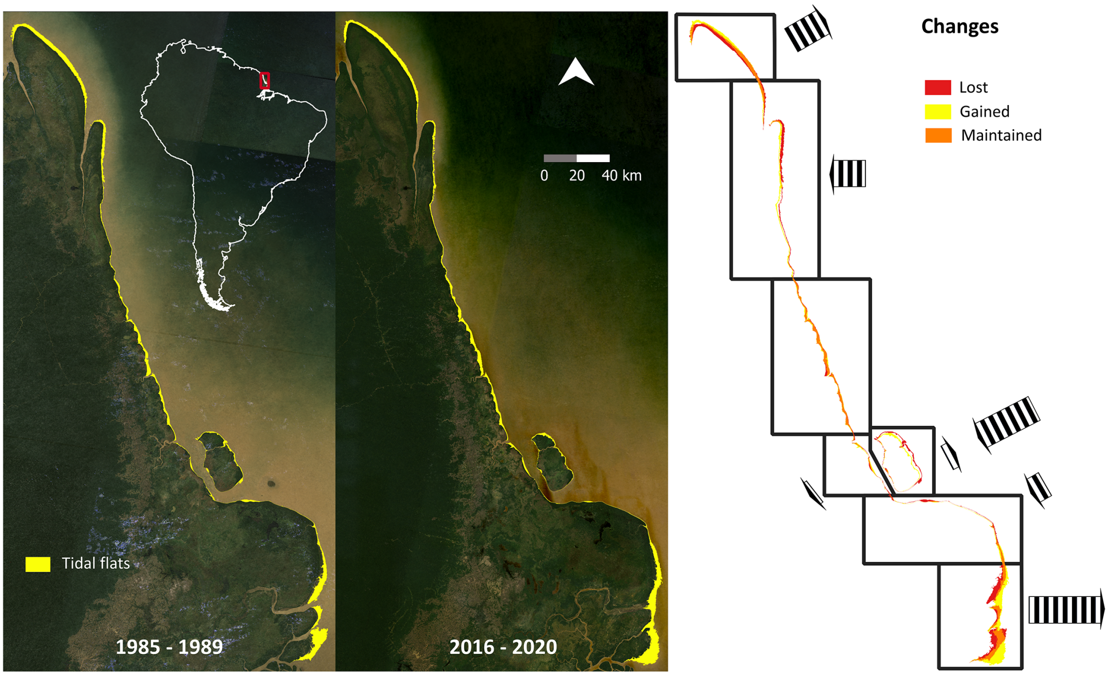

Figure 1. Tidal flat distributional changes between the late 1980s and the period covering the shorebird surveys. Arrows in the right panel indicate the extent of the landward or seaward movement of tidal flats in each region of the study area, with each division on the scale representing 100 m. Tidal flat distributions were derived from Landsat imagery (see methods for details). The inset map shows the location of the study area within South America. The background images were created by averaging true-color Landsat composites from four scenes covering the study area. The left panel is based on 148 Landsat 5 images acquired between 1985 and 1989, while the right panel uses 160 Landsat 8 images acquired between 2016 and 2020. These Landsat datasets are available through GEE, courtesy of the US Geological Survey.

The climate is warm and humid, characterized by an annual average temperature of 26 °C and 3000 mm of rainfall, which is particularly concentrated from January to May [25]. Coastal habitats include freshwater lakes and marshes, saltmarshes, mangrove forests, and tidal flats, with freshwater marshes covering the largest area [29]. Human population density is less than one inhabitant per km^2, with the main cities, Oiapoque, Calçoene and Amapá, comprising ca. 50 000 people [30]. The primary economic activities are livestock farming and fisheries [31]. The Amapá coastline is strongly influenced by sediment redistribution and freshwater discharge from the Amazon River delta, located in the south of the study area (figure 1). A large portion of the river plume sediment is transported northwest by the North Brazil Current, thereby forming extensive mudflats along the coast [32]. The entire coast is exposed to semidiurnal macrotides, reaching tidal amplitudes of as much as 10 m in its middle section [25]. Tidal forces, river discharge, wind and currents all contribute to the highly dynamic processes of coastal erosion and accretion, channelization, flooding, and salinization observed in the study area [25]. Evidence of saltwater intrusion has been reported in recent studies and by the local residents. Increased salinity was observed in Piratuba Lake (1.684° N, −50.138° E) in 2016 [28], and severe salinization of Bom Nome Lake (1.949° N, −50.624° E) over the last decade was reported by people from local communities and the resulting environmental changes were documented through satellite imagery [9]. Furthermore, large-scale inland migration of mangroves was evidenced by satellite imagery time series analysis since the mid-1980s, with the migration speed matching the patterns of SLR acceleration observed in gauge data recorded in Cayenne, French Guiana [9].

2.2. Aerial surveys

In late January of 2018 and 2020, we conducted low-altitude flights in a high-wing Cessna aircraft to count shorebirds distributed along the edge of tidal flats throughout the study area. We adopted the survey protocol of Morrison and Ross [24], which was developed specifically to monitor wintering populations of shorebirds in South America. Flights were timed to match periods close to high tide (±2 h), but avoiding the high tide maximum, to ensure that the exposed tidal flats were narrow enough to be surveyed in a single passage. The plane flew in a general NNW-SSE direction but closely following the water edge and keeping the vegetated shoreline within a distance ranging from ca. 50–500 m. In sections with wider exposed tidal flats, the plane either took a median course between the water edge and the vegetated shoreline or made several passages to ensure the entire area was surveyed. The two observers, who conducted both surveys, sat on the landward side of the airplane to have a clear view of the exposed tidal flats. The airplane flew under 50 m above ground level at a speed of ca. 160 km h^{-1}. Shorebirds typically took flight slightly ahead of the airplane along the shoreline, allowing observers to count them individually or estimate flock sizes. Shorebirds were identified based on their size, morphology and behavior. Although it was not always possible to accurately identify small sandpipers (Scolopacidae) in large flocks to the species level during the aerial surveys, species other than the semipalmated sandpiper (*Calidris pusilla*) are nearly absent in the study area. This was supported by previous aerial surveys conducted by Morrison and Ross [24], and ground surveys and mist netting conducted by our team. Sanderlings (*Calidris alba*) and spotted sandpipers (*Actitis macularius*) may have been occasionally misidentified as semipalmated sandpipers. However, these two species represented less than 0.3% of the total number of small shorebirds counted (table S1), posing minimal potential bias to our analysis and conclusions. Medium-sized shorebirds were dominated by lesser and greater yellowlegs (*Tringa flavipes* and *T. melanoleuca*), which typically associated in mixed flocks, preventing species-level quantification. The remaining medium-sized shorebirds included low numbers of black-bellied plovers (*Pluvialis squatarola*) and ruddy turnstones (*Arenaria interpres*), and a relatively high number of individuals that could not be identified (26%, table S1), which were excluded from further analysis. Among large shorebirds, hudsonian whimbrels (*Numenius hudsonicus*) and willets (*Tringa semipalmata*) were present in low numbers and their identification was straightforward. Shorebird identifications and count estimates were recorded on a voice recorder and GPS positions were marked periodically to delimit the survey sectors, typically at notable landmarks such as river mouths or promontories. After each flight, the results from both observers were compared to reassess species identifications and count estimates for the larger flocks. However, we only used the final results of a single observer to avoid data pseudoreplication affecting our analyses. Data analysis focused on the distribution of semipalmated sandpipers, for being the most abundant species by far (table S1), and the remaining shorebird species collectively (hereafter referred to as 'other shorebirds'). In this species group, we excluded spotted sandpipers as this species was rarely found on tidal flats, preferring marginal microhabitats such as creeks and debris from eroded mangroves.

2.3. Mapping tidal flats

The distribution of tidal flats in the late 1980s and the period covering the aerial surveys was mapped from Landsat imagery (Landsat 5 and 8, Collection 2, Tier 1 and 2) using Google Earth Engine (GEE) [33]. Since the tidal cycle varies considerably across the study area (with ca. 4 hour delay between the SSE and NNW extremes), low tide images do not accurately represent the maximum extent of tidal flats. To overcome this issue, we used a methodological framework (proposed by [34]) that discriminates tidal flats from neighboring habitats based on their flooding dynamics. The flooding dynamics of tidal areas were derived from the standard deviation of the normalized difference water index (NDWI) from stacks of images acquired at different tidal stages. As the position of the waterline varies within the stack of images, tidal flats show a high NDWI standard deviation compared to terrestrial and permanent water areas. However, this metric presented indistinct boundaries of tidal flats in some regions of our study area. To improve the discrimination of these boundaries, we employed a random forest classifier (function smileRandomForest of GEE) that combined NDWI standard deviation with additional metrics, namely the mean normalized difference vegetation index, the mean NDWI and the mean values of the bands with spectral correspondence between Landsat 5 and Landsat 8 (Landsat 5: bands 1–5, 7; Landsat 8: bands 2–7). We performed this analysis by first selecting the images to be compiled into the image stacks. To map tidal flats in the late 1980s, we used stacks of Landsat 5 images acquired from 1985 to 1989. For the period overlapping with the aerial surveys, we used stacks of Landsat 8 images acquired from 2016 to 2020. The 5 year period of these stacks was necessary due to the limited number of images available for the study area, as the vast majority were unusable because of high cloud cover. Some Landsat 5 images had positional errors, often being misplaced by tens or even a few hundreds of pixels. We corrected the positions of these images using the translate function of GEE, employing winding sections of small rivers as landmarks. Images showing latitude and longitude distortions greater than two pixels were excluded. The final stack for the 1985–1989 period included 33–40 images (depending on the scene), while the stack for the 2016–2020 period included 40 images for each scene. The selected images were masked for clouds using QA bands, followed by a visual inspection. The stacks were then processed to generate the metrics for the random forest classifier. To train and validate the classifier, we distributed 3000 sampling points over true color composites of low-tide images that undoubtedly corresponded to land, water or tidal flats. Of these 3000 points, 2000 were used to train the classifier and the remaining 1000 were used for validation. We then converted the classifications into shapefiles and selected the large polygons corresponding to tidal flats that were contiguous with the coastline. Small polygons located offshore were excluded, as they likely represent patches of highly turbid water misclassified as tidal flats, which is a common issue in tropical areas with turbid river discharges [35]. Nevertheless, these polygons accounted for less than 2.5% of the overall area identified as tidal flats in both classifications. We also excluded a few small offshore tidal banks as they were far from the counting sectors of the aerial surveys. The final tidal flat distributions for 1985–1989 and 2016–2020 were intersected to distinguish the areas resulting from marine transgression from the remaining tidal flats.

2.4. Prey availability and sediment characterization

In January 2023, we conducted a land expedition to Maracá Island (see location in figure S1) to survey shorebird prey availability and characterize sediments in transgressed areas and adjacent tidal areas (serving as controls). Sediment samples were collected in the tidal flats of the island and the nearby continental margin (figure S1). Most areas were sampled by boat during high-tide using a sampling corer with a 2 m long handle. In areas with firm sediments, we walked between sampling locations during low-tide. Sampling locations were sparsely distributed, with an average distance of 448 m between neighboring points, and never closer than 170 m (figure S1). We collected 75 sediment cores (70 cm^2 and 20 cm deep) to assess prey availability, including 25 in transgressed areas and 50 on other tidal flats (figure S1). For each core sample, we separated the top 5 cm of sediment and sieved it through a 0.5 mm mesh, while the remaining section of the core (5–20 cm depth) was sieved through a 1 mm mesh. This procedure is commonly adopted to survey prey availability for shorebirds as small macroinvertebrates are considered unavailable if living at depths below 5 cm [36]. Macroinvertebrates extracted from the sediment samples were preserved in 70% alcohol and taken to the laboratory, where they were identified to the lowest possible taxonomic level. We collected additional core samples to quantify sediment granulometry (9 in transgressed areas and 12 on other tidal flats) and to measure sediment relative penetrability (11 in transgressed areas and 14 on other tidal flats) (figure S1). For granulometry, 80 ml of sediment was collected from the top 2 cm of each core. In the laboratory, the sediments were dried to a constant weight and sieved through a 63 μm mesh to quantify the percentage of fine sediments (silt and clay). The relative penetrability of the sediments was measured in the field by dropping a metal rod (15 cm, 12 g) from a height of 1 m onto the top of the sediment core and measuring the depth of penetration. We also collected 30 fresh droppings from semipalmated sandpipers observed feeding on the tidal flats. These samples were collected during the receding tide at two locations where birds gathered in large, concentrated flocks, with no other bird species present. In the laboratory, each Eppendorf tube (1.5 ml) containing an individual dropping was filled with water, homogenized, and two drops of the liquid were spread on a microscope slide using a 3 ml pipette. The slides were examined under a microscope at 400× magnification to search for polychaete setae and other small structures of prey. The remaining sample was observed under a stereomicroscope to search for larger remnants of prey. All remnants of prey were identified using a reference collection created from the benthic macroinvertebrates collected in the core samples.

2.5. Data analysis

Shorebird counting sectors were delimited in GIS from the GPS positions recorded during the aerial surveys and the airplane flight track (see figure 2). These sectors were then intersected with the maps of tidal flats to calculate the percentage of each sector covered by transgressed areas. The relationship between the number of shorebirds counted in the surveys and availability of transgressed areas within the counting sectors was modeled using generalized linear mixed models (GLMMs). The models were fitted in R [37] using the glmmPQL function from the MASS package [38]. The spatial autocorrelation in shorebird numbers was accounted for in the models by using a Gaussian correlation structure based on the coordinates of the counting sectors. The survey year (2018 or 2020) was included as a random intercept factor to account for the interannual variation in shorebird numbers. Since the counting sectors varied in size, we included sector area as an offset factor. Models were fitted with a negative binomial distribution with theta = 0.5, which accurately reflects the distribution of shorebird counts in large sectors, where zeros and low numbers are more frequent than larger numbers.

Two sets of models were built. In the first set, we used the percentage of counting sectors covered by transgressed areas as a continuous predictor. This allowed us to use data from all counting sectors (n = 242). In the second set of models, we selected counting sectors that were either fully covered by transgressed areas (n = 55) or had no cover at all (n = 47). In this case, tidal habitat was included in the models as a categorical predictor. These models enabled a more direct comparison with the results for benthic macroinvertebrates. In both sets of models, we built separate models for the semipalmated sandpiper and for the remaining shorebirds as a group.

3. Results

The classifications of tidal flats from Landsat images were generally highly accurate. Overall accuracy was 0.98 for both the 1985–1989 and 2016–2020 tidal flat distributions. The user's accuracy (sensitive to errors of commission) was above 0.96 for the three cover classes (water, land and tidal flats) for the 1985–1989 distribution and was above 0.97 for the 2016–2020 distribution (table S2). The area covered by tidal

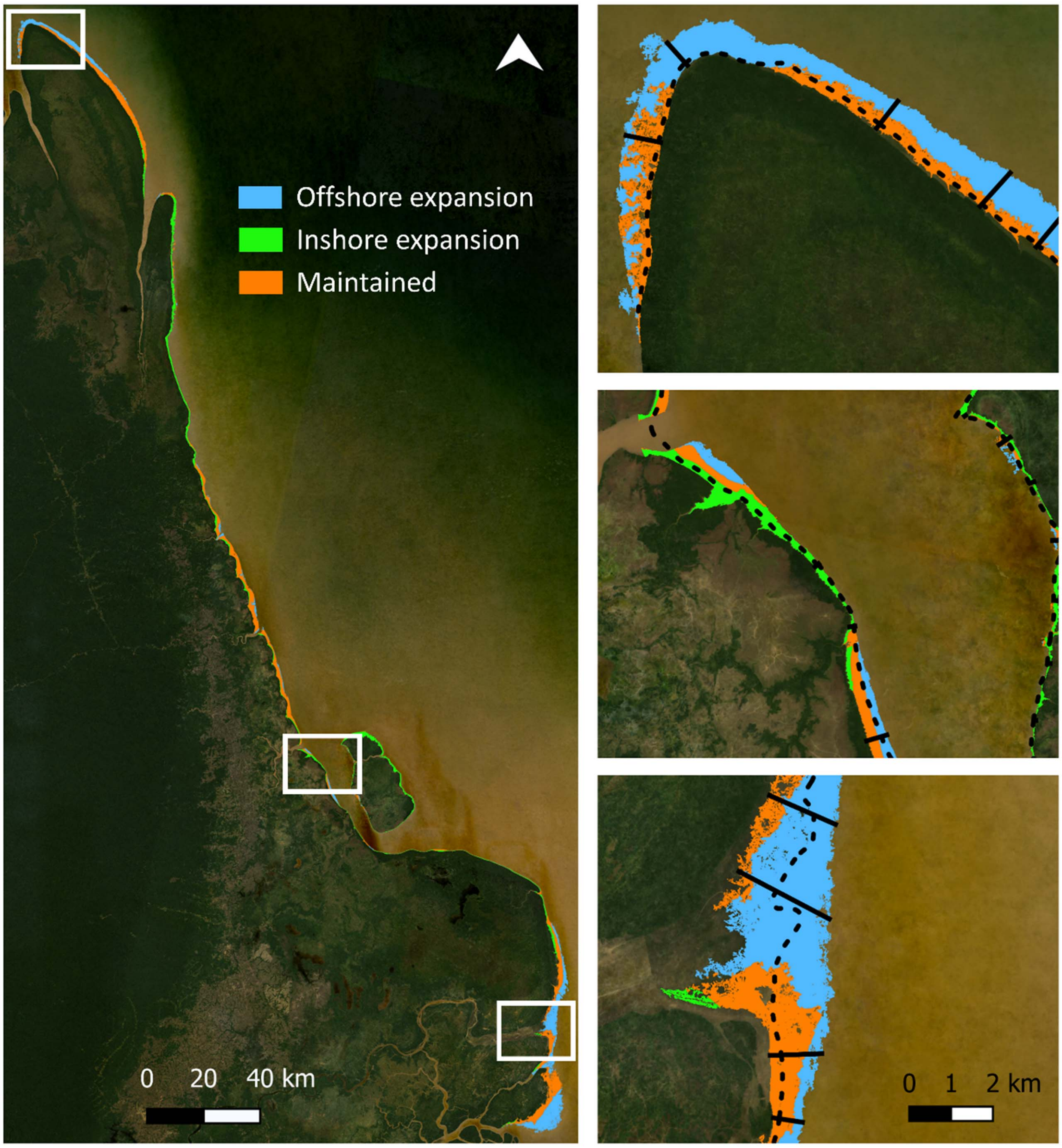

Figure 2. Origin of the tidal flats surveyed for shorebirds in 2018 and 2020. We distinguished tidal flats that were maintained since the late 1980s from those that have formed either landward or seaward since then. Right panels show the counting sector limits in 2020 (solid lines) and the trajectory of the airplane (dashed line). Tidal flat distributions used in this classification were derived from Landsat imagery (see methods for details). The background image was generated by averaging 160 true-color Landsat 8 composites from four scenes acquired between 2016 and 2020. This dataset is available through GEE, courtesy of the US Geological Survey.

flats increased by 6% from 1985–1989 to 2016–2020 (figure 1). There were also significant changes in the location of tidal flats. For most of the coastline (ca. 70%) there was a landward migration of tidal flats, ranging from ca. 10 m in the middle section of the study area to nearly 1.5 km in the seaside coast of Maracá Island (figure 1). A seaward movement of tidal flats occurred near the mouths of large rivers, namely, the Oiapoque at the northern limit of the study area, and the Araguari and Amazon at its southernmost part (figure 1). The tidal flats originated from marine transgression since the late 1980s occupied ca. 20% of the tidal flat area by the time the aerial surveys were conducted (figure 2).

During the aerial surveys, we counted 79 803 shorebirds, with the relative abundance of the different species being consistent between the two survey years (table S1). The semipalmated sandpiper was by far the most abundant species, representing 91% of the shorebirds counted (table S1). Shorebirds clearly avoided tidal flats resulting from marine transgression. The number of birds decreased significantly as the percentage of counting sectors covered by transgressed areas increased (figure 3). This pattern was observed for semipalmated sandpiper as well as for the remaining shorebird species combined (figure 3, see table S3 for model statistics). Our models predicted that shorebird densities in

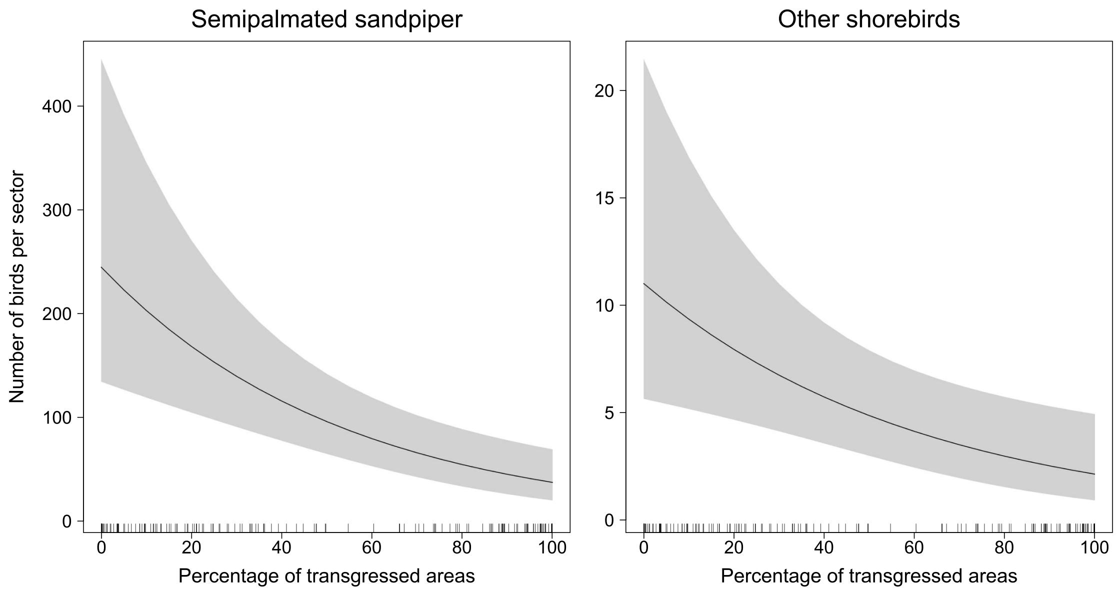

Figure 3. Decline in shorebird use of tidal flats with an increasing percentage of area resulting from marine transgression. Plots represent effects of GLMMs that account for interannual variation and spatial autocorrelation in bird numbers (see methods for model details). Shading represents 95% confidence intervals. Under the species group 'other shorebirds' we included lesser and greater yellowlegs, black-bellied plover, ruddy turnstone, hudsonian whimbrel, willet and sanderling.

sectors fully occupied by transgressed areas were nearly one order of magnitude lower (on average) than those sectors lacking this habitat (figure 4, see table S3 for model statistics). These results were reflected in the differences found for the abundance of benthic macroinvertebrates (figure 4). The crustacean *Discapseudes surinamensis* stood out as the most abundant benthic macroinvertebrate species in the sediment samples (table S4), and its remains were identified in 90% of the fecal samples of semipalmated sandpipers, with abundant exoskeleton fragments present in most samples. The abundance of this species was nearly one order of magnitude lower (on average) in transgressed areas than in other tidal flats (figure 4). We also found significant differences with the same trend for the remaining species of macroinvertebrates pooled together (figure 4). The polychaete *Alitta succinea* was the only species showing significantly higher densities in transgressed areas, but this species was globally scarce in the study area (table S4). Setae of Nereididae polychaetes were found in 53% of the fecal samples, although in very low amounts, suggesting that these prey were incidental.

Sediment composition was similar in both types of tidal flats, with silt and clay (i.e. particles $< 63~\mu$m) representing 80%–99% of the sediment dry weight in all samples collected (transgressed areas: mean = 91%, range = 80%–99%; other tidal areas: mean = 91%, range = 82%–99%, table S5). However, sediments in transgressed areas were denser than those in the remaining tidal flats, with penetrability being three times lower (transgressed areas: mean = 3.0 cm, range = 0.5–8.0 cm; other tidal areas: mean = 9.2 cm, range = 6.0–13.0 cm; t test: $t = 7.4$, $df = 22.9$, p-value < 0.001, table S5).

4. Discussion

The inland migration of coastal wetlands is a global phenomenon triggered by SLR [6, 21]. While this ecological adaptation may help preserve the extent of coastal wetlands, substantial ecological transformations are expected to occur within these ecosystems [7, 21]. In this study, we provide evidence that tidal flats on the coast of the Brazilian Amazon, distant from river mouths, are generally moving inland (figure 1). This corroborates a previous study in the same area showing that mangrove forests are migrating inland at the pace of SLR [9]. In three areas under the influence of large river mouths, we observed the expansion of tidal flats seaward, which might be explained by the increase in sediment loads carried by these rivers due to escalating deforestation within their drainage basins [39]. The expansion of tidal flats near river mouths was the main cause of the slight increase (ca. 6%) in overall tidal flat coverage since the late 1980s.

The inland migration of tidal flats observed far from river mouths resulted from the combined effect of erosion on the seaside edge and marine transgression over terrestrial habitat (figure 1, see [40]). Despite the tidal flat area being conserved, the characteristics of the tidal flats changed considerably due to the increasing occupancy of transgressed areas. The contrasting aspect of this new type of tidal flats became evident during aerial surveys through its rutted and uneven surface, and the abundance of

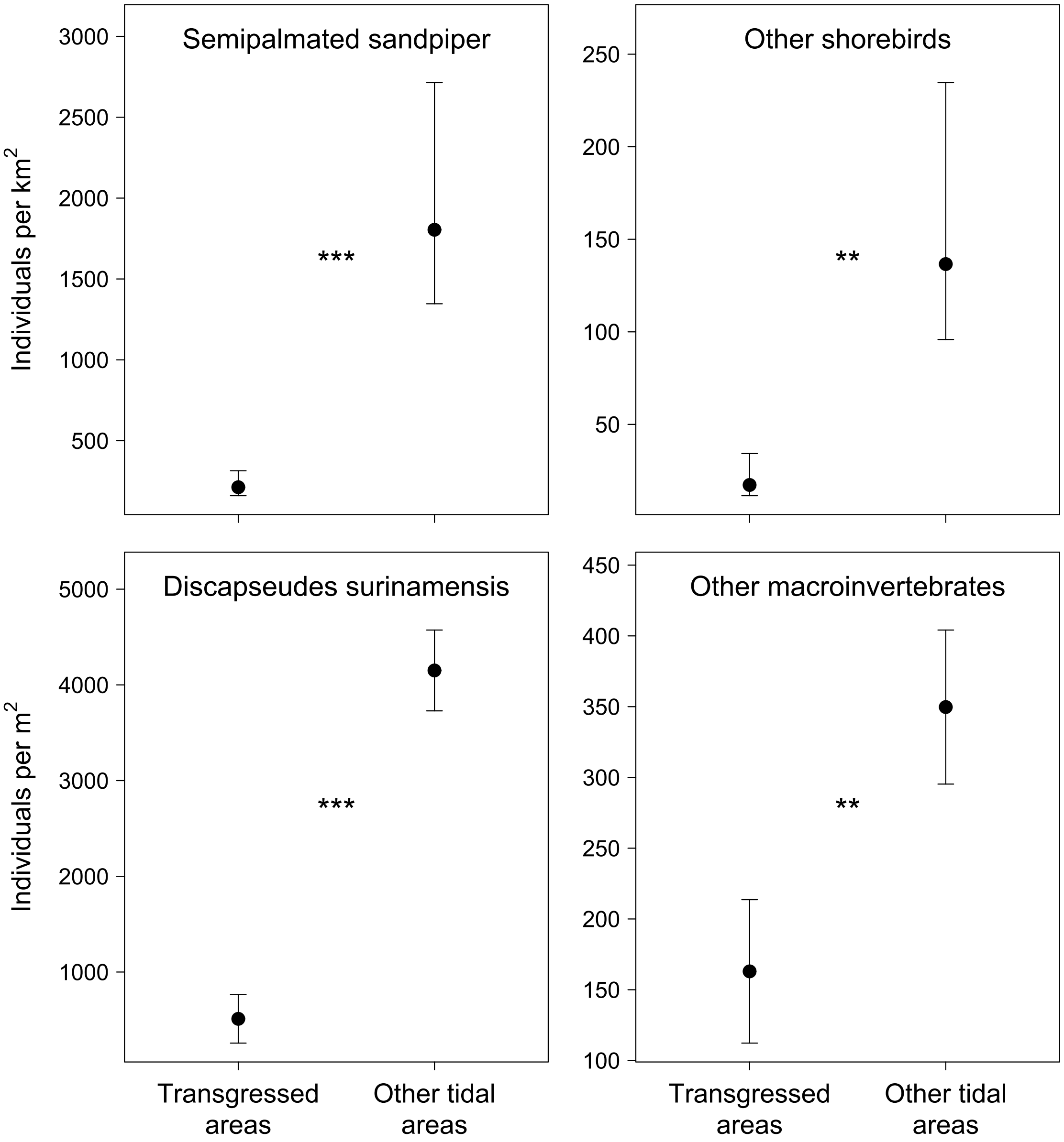

Figure 4. Bird and benthic macroinvertebrate densities in tidal flats resulting from marine transgression compared to the remaining tidal flats present in the study area. Top plots represent effects of GLMMs that account for interannual variation and spatial autocorrelation in bird numbers (see methods for model details). Model estimates (bird numbers) were divided by the mean area of counting sectors to obtain densities. Error bars represent model standard errors. Under the species group 'other shorebirds' we included lesser and greater yellowlegs, black-bellied plover, ruddy turnstone, hudsonian whimbrel, willet and sanderling. Bottom plots represent mean and standard error of macroinvertebrate densities recorded in sediment cores collected in both habitats. Under the 'other macroinvertebrates' category we included polychaetes, amphipods, bivalves, tube-dwelling anemones (Ceriantharia), oligochaetes, ribbon worms (Nemertea), and planarians (see table S4 for species discrimination). Statistical significance: ** $p < 0.01$; *** $p < 0.001$.

mangrove trunks embedded in the sediments (figure S2). Our field measurements showed that surface sediments were more consolidated in transgressed areas than in the remaining tidal flats, although their granulometry was similar. This raises the question of whether this new type of tidal flats would allow for colonization by benthic macroinvertebrates, which sustain thousands of shorebirds that migrate from high-latitudes of the northern hemisphere to spend the non-breeding season in this region. By analyzing the distribution of migratory shorebirds along a stretch of tidal flats of ca. 630 km, we demonstrated that these birds clearly avoid tidal flats resulting from marine transgression. Shorebird numbers declined with the increased occupancy of tidal flats by transgressed areas (figure 3). Shorebird densities were nearly one order of magnitude lower in tidal flats entirely occupied by transgressed areas compared to those showing no transgression (figure 4). Our results further indicated that the low use of transgressed areas by migratory shorebirds was due to the low abundance of prey. Sediment samples collected from a section of the study area revealed that the abundance of benthic macroinvertebrates was much lower in transgressed areas than in other tidal flats (figure 4). The response of shorebirds' habitat use to prey availability was clearly demonstrated for the semipalmated sandpiper, which was found to feed preferentially on the crustacean *D. surinamensis* based on fecal analysis. The very low abundance of this crustacean in transgressed areas was reflected by the low numbers of semipalmated sandpipers, with both species presenting densities one order of magnitude lower in transgressed areas than in other tidal flats (figure 4). These results lead us to conclude that, although the inland migration of coastal wetlands may contribute to the maintenance of overall tidal flat area, the transformation of tidal flats caused by such migration may translate into considerable loss of feeding habitats for non-breeding migratory shorebirds. It should be noted, however, that transgressed areas may be expected to evolve as SLR progresses and eventually become adequate habitat for benthic macroinvertebrates that serve as feeding resources for shorebirds [5, 21].

Several studies have argued that the inland migration of tidal habitats could ameliorate habitat loss for shorebirds and recommended facilitating such movement in areas protected by coastal defenses as important conservation actions [5, 16, 17, 41, 42]. While we agree that such actions may help mitigate the effects of SLR on coastal wetlands and should be encouraged, our results clearly indicate that this may not be enough to conserve feeding habitats for shorebirds within a scale of decades. We further recommend that these actions be accompanied by the conservation and restoration of tidal vegetation, which plays a key role in the deposition of soft marine sediments and may help to accelerate the transformation of transgressed areas into tidal areas suitable for the establishment of benthic macroinvertebrates [21, 43].

It is consensual within the scientific community that the generalized declines observed in migratory shorebirds are caused by multiple factors occurring at different stages of their annual cycle [14]. Furthermore, detrimental factors acting at specific areas along migratory flyways may propagate through carry-over effects [44, 45]. A wide range of impacts on migratory shorebirds result from increasing human disturbances to coastal wetlands in developed regions [13, 14]. However, it becomes evident from our study that even while utilizing remote, pristine coastal areas, migratory shorebirds may be exposed to broader scale human impacts, such as those resulting from SLR.

In conclusion, we have demonstrated that the inland migration of tidal flats in response to SLR leads to their gradual occupation by areas created through marine transgression, which may be unsuitable as feeding grounds for migratory shorebirds over the course of several decades. This phenomenon constitutes a form of habitat loss not previously identified in shorebird research. We emphasize that, given the global scale of SLR, this type of habitat loss may be widespread and will likely worsen in the future. Further research is needed to elucidate the geographical extent of this phenomenon and to identify additional impacts of ongoing environmental changes in remote coastal wetlands on migratory shorebirds.

Data availability statement

The field data that support the findings of this study are openly available at the following URL/DOI: https://doi.org/10.5281/zenodo.13895301. The Landsat imagery used in remote sensing analysis can be freely accessed through the Google Earth Engine platform (https://earthengine.google.com).

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Ethics statement

The ethical procedures for this study and the access to protected areas were approved by Brazilian authorities, namely ICMBio (SISBIO 42418 and 78429), CNPq (Portarias 162–25/02/2016 and 849–10/05/2022) and CEUA of the Federal University of Pará (license: 8335300921).

Author contributions

Carlos D Santos: Conceptualization; methodology; investigation; data curation; formal analysis; writing—original draft. **Danielle Paludo:** Methodology; investigation; data curation; writing—review & editing. **Paulo Silvestro:** Funding acquisition; writing—review & editing. **José O. Monteiro:** Investigation; data curation; writing—review & editing. **Paulo P G Pachelle:** Investigation; data curation; writing—review & editing. **Verônica Oliveira:** Investigation; data curation; writing—review & editing. **Jason A Mobley:** Funding acquisition; writing—review & editing.

Conflict of interest

The authors have no conflict of interest to declare.

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