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Habitat Suitability for a Unique, Fully Marine American Manatee (*Trichechus manatus*) Population Primarily Depends on Presence of Submarine Freshwater Springs

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ABSTRACT

The American manatee (*Trichechus manatus*) requires freshwater mainly from rivers and springs to maintain osmoregulatory balance in saline environments. However, in Brazil's semi-arid Potiguar Basin, manatees now rely solely on submarine freshwater springs because hypersaline estuaries have become unsuitable sources of freshwater. We applied MaxEnt modeling to presence-only data (sightings and filtered telemetry records) to produce habitat suitability maps and identify the environmental conditions driving habitat use. Telemetry locations were spatially and temporally thinned and subsampled to balance individual contributions, and alternative thinning scenarios were evaluated—while the model with the lowest level of spatial filtering showing the most stable performance was retained for inference. Model performance and fit were high (AUC = 0.979; CBI = 0.943, training gain = 2.76), and model suitability was strongly structured by proximity to submarine springs, with predicted probability declining sharply beyond 4–8 km. Seagrass presence contributed secondarily to suitability, whereas the other variables showed limited independent explanatory power at the regional scale. Suitable habitat was highly localized, comprising approximately 4% (301 km^2) of the modeled coastal area and concentrated near Icapuí (Ceará) and Areia Branca (Rio Grande do Norte). These findings reveal the strong ecological constraints shaping this fully marine manatee population and highlight the critical role of submarine freshwater springs and seagrass meadows in sustaining manatee presence in hypersaline coastal systems. Protecting these key resources is essential for conservation planning in a region facing increasing freshwater limitation and expanding offshore development.

1 | Introduction

The American manatee (*Trichechus manatus*), referred to hereafter as “manatee,” is a large herbivore that grazes on aquatic vegetation and requires access to freshwater to maintain physiological balance in saline environments (Deutsch et al. 2022; Rathbun et al. 1990). Although the extent of their freshwater dependence for osmoregulation is not clear (Reynolds III

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et al. 2018), evidence suggests that freshwater availability is particularly important in regions where hypersaline conditions prevail (Ortiz et al. 1999).

Historically, manatees along the northeastern Brazilian coast were heavily affected by hunting and habitat degradation—factors widely recognized as contributing to low population size, fragmentation, and local extirpations (Domning 1981; Lima 1997; Luna et al. 2008). Despite decades of legal protection, these populations remain vulnerable, particularly in environmentally constrained regions such as the Potiguar Basin (Meirelles et al. 2024, 2022).

The Potiguar Basin, located along the semi-arid coast of northeastern Brazil (Figure 1), presents a challenging environment for manatees. This region is characterized by small rivers, limited fluvial discharge, and naturally hypersaline estuaries with pronounced seasonal salinity fluctuations (Soares et al. 2021; Valentim et al. 2018). Historically, manatees appeared to have used these estuarine habitats (Choi-Lima et al. 2017), but the increasing intensity and persistence of hypersaline conditions—driven by declining river flow and cumulative human pressures—have reduced their suitability (Soares et al. 2021). As a result, manatees in the Potiguar Basin now appear to rely primarily on submarine freshwater springs in the ocean as their main source of freshwater (Aquasis 2006; Choi-Lima et al. 2017).

Although submarine freshwater springs have not been directly assessed in terms of vulnerability, the coastal aquifers that sustain them are increasingly affected by salinization (Araújo et al. 2023) and contamination resulting from inadequate sanitation infrastructure (Maia et al. 2017). Additionally, projected increases in drought frequency under climate change scenarios (Marengo et al. 2020) may further reduce groundwater recharge in this semi-arid region, potentially limiting freshwater supplied to these submarine springs. While hypersalinization has not yet been formally recognized as a threat to manatees, emerging evidence from semi-arid coastal systems suggests that it may pose increasing risks through both physiological stress (Meirelles et al. 2024) and the loss of seagrass habitats (Soares et al. 2021).

Beyond freshwater constraints, Potiguar Basin manatees have a specialized diet composed primarily of seagrass, especially shoal grass (*Haludule wrightii*) (Carvalho et al. 2009; Ciotti 2012). This contrasts with the more diverse aquatic vegetation consumed by manatees elsewhere in South America (e.g., Arévalo-González

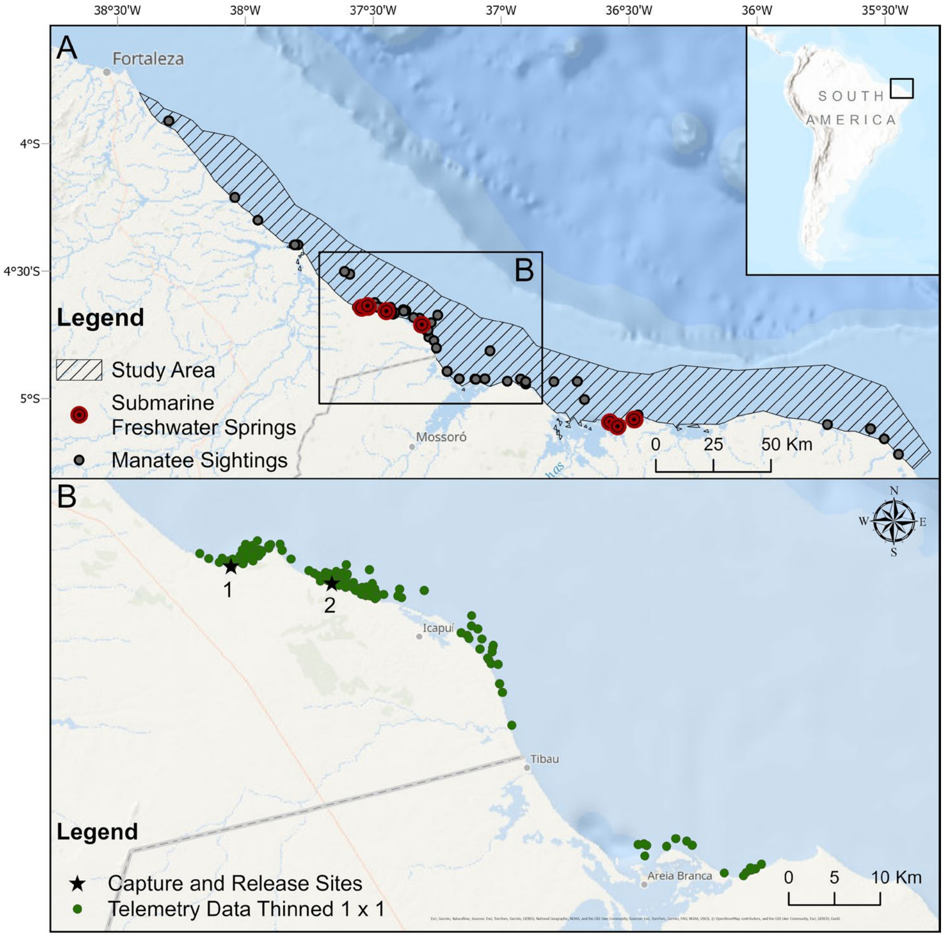

FIGURE 1 | Study area and spatial distribution of American manatee records along the semi-arid coast of northeastern Brazil. (A) Regional overview of the study area and compiled sighting records and submarine freshwater spring locations. (B) Enlarged view of the central portion of the study area showing five wild manatees telemetry data thinned (grid 1×1, one per day per animal) and balanced (33 records per animal, except Gabi) and the two sites where the animals were captured and released (1. Retirinho: Redonda, Icapuí, and Gabi; 2. Picos: Adao and Eva).

et al. 2025). The limited availability of both freshwater and diverse food sources underscores the ecological distinctiveness of the Potiguar Basin and the environmental pressures that have shaped the region's unique patterns of manatee distribution and habitat use.

Compounding these ecological and physiological constraints, the manatee population inhabiting the Potiguar Basin is small ($n = 193$) and sparsely distributed (0.03 individuals/km^2) (Petrobras 2014), conditions that increase its vulnerability to additional stressors. The region also exhibits one of the highest incidence of neonate strandings for the species—posing further challenges to recruitment and population recovery (Meirelles et al. 2024).

Throughout the study area, conservation efforts for the American manatee have long included monitoring, rescue, rehabilitation, and release programs (Meirelles and Carvalho 2016). Recent research has identified key drivers of resource selection within the state of Ceará (Normande et al. 2026), yet spatially explicit species distribution models capable of predicting habitat suitability across the broader regional landscape remain limited.

In environmentally constrained systems, such as the Potiguar Basin, understanding the factors that influence manatee presence is essential for determining how habitat use is shaped by limited freshwater availability and scarce food resources. Without this information, conservation actions may fail to protect the habitats most critical to sustaining manatee populations under ongoing environmental change.

To address these knowledge gaps, we used a species distribution modeling approach (Maxent) to analyze manatee presence data derived from sightings and telemetry in relation to environmental variables. Our objectives were to (1) identify the key drivers of manatee presence in the Potiguar Basin and (2) map areas of suitable habitat. Such predictive models complement ongoing conservation efforts by providing a spatial framework to support habitat-focused planning.

2 | Methods

2.1 | Study Area

The Potiguar Basin lies along the northeastern coast of Brazil, extending from Aquiraz in the state of Ceará to Touros in the state of Rio Grande do Norte (Figure 1). This semi-arid zone is characterized by a mix of coastal habitats, including estuaries, sandy beaches, seagrass beds, and mangroves. Freshwater input is limited due to small rivers and intermittent rainfall, which contributes to hypersaline conditions in many estuaries (Soares et al. 2021). We restricted our analysis to the 10-m isobath because manatees have not been reported in deeper waters. This yielded a study area covering approximately 7700 km^2.

2.2 | Manatee Presence Data

The presence data we used included only direct evidence of manatee occurrence, such as sightings (from land-based, boat, and aerial surveys) and telemetry data collected from 5 wild manatees captured and tagged with GPS devices in the state of Ceará (see more details in Normande et al. 2024) (Table 1). Stranding records were not included because they can overestimate suitable habitat areas Meirelles et al. 2026.

Telemetry and sighting records differ in their statistical structure. Most notably, telemetry data represent repeated measures from known individuals and are therefore subject to spatial and temporal autocorrelation (Boyce et al. 2010), whereas sightings reflect independent survey detections. Because our objective was to infer population-level habitat suitability rather than individual-level space use, both data types were treated as complementary sources of environmental presence information.

Telemetry data consist of repeated locations from the same individuals and therefore reflect continued use of the same environmental context rather than independent habitat-use events. To ensure biological comparability with survey-based sightings and to limit the influence of individual movement histories, telemetry data were filtered in sequential steps. First, we spatially filtered locations to retain at most one telemetry location per individual within each grid cell, reducing pixel-level redundancy and spatial clustering. We defined grid cell size as a multiple of the environmental raster resolution (463 m), and evaluated a range of spatial filtering scales from 1 × 1 to 5 × 5 grid cells. Second, we applied a temporal filter for the remaining locations for each individual, retaining at most one location per day. This step treats each retained telemetry point as a single daily decision of habitat use rather than as a raw GPS fix, thereby reducing temporal autocorrelation while preserving between-individual representation.

After spatial and temporal thinning, the number of retained telemetry locations still varied among individuals due to differences in tracking duration and space use. To equalize individual contributions of telemetry data, the maximum number of telemetry locations per individual was set to the minimum number observed among these individuals (except individual Gabi that had few data points), and locations were randomly subsampled to this value. This approach ensures comparable individual-level contribution while preventing dominance of individuals with longer tracking histories.

Telemetry filtering was implemented in R (v 4.4.1; R Core Team 2024) using the packages raster (Hijmans 2025), dplyr (Wickham et al. 2023), and lubridate (Grolemund and Wickham 2011). All data-processing and filtering scripts are provided in the Supporting Information.

It was not possible to determine whether some sighting records corresponded to telemetry-tagged individuals. We therefore spatially and temporally filtered and balanced the telemetry data across individuals to reduce autocorrelation and prevent disproportionate representation of tracked animals. Furthermore, because MaxEnt models presence against background environmental conditions rather than detection frequency (Phillips et al. 2006), potential overlap between data sources is unlikely to bias results unless it substantially alters the range of environmental conditions represented in the dataset.

TABLE 1 | Data sources and citations used in this study.

Type of survey	Total surveyed area	Year	Length of survey in the study area	Covered the whole study area?	Manatee records in the study area	Source
Aerial: Parallel transects	From Aquiraz (CE) to Touros (RN), perpendicular transects	April 2014	3453 km	Yes	33	Petrobras (2014)
Aerial: Strip-transect aerial	From the states of Piauí to the state of Alagoas	January–April 2010	Not reported	Yes	9	Alves et al. (2015)
Aerial	From Fortaleza (CE) to Ponta do Mel (RN)	July and August 2003	(2434.2 km)	No	10	Fundação Mamíferos Aquáticos (2003)
Linear aerial transects parallel to the coastline	From Pontal do Maceió (CE) to Tibau (RN). 900 and 1200 m from shore	June 2003 to October 2004	540 km (estimated)	No	9	Aquasis (2006); Costa (2006)
Linear boat transects parallel to the coastline	From Retirinho (CE) to Tibau (RN)	August 2003 to November 2004	500 km (estimated)	No	16	Aquasis (2006); Costa (2006)
Zig-zag transects, between the coast and 5 m isobath	From Retiro Grande (CE) to Ponta do Mangue (RN)	April to September 2001	3000 km	No	5	Aquasis (2001)
Land-based	Picos and Retiro Grande (CE)	2002	—	No	2	(Alves 2007)
Telemetry—5 wild manatees	—	May 2012 to April 2014	—		5565	Normande et al. (2024); Petrobras (2014)

Abbreviations: CE = Ceará; RN = Rio Grande do Norte.

2.3 | Explanatory Variables

Before modeling, we assessed multicollinearity among the candidate predictors to ensure that no single predictor's effect was overshadowed by highly correlated variables. For pairs of variables with Pearson correlation values > 0.75, we retained the variable deemed more biologically relevant to the species' presence (Figure S1). Justifications for the selected predictors, along with their sources and derivation processes, are provided in Table 2. Due to the relatively small geographic size of our study area and the lack of variation in some oceanographic variables, we did not include sea surface temperature and salinity in the analysis, although they have been identified as important variables at larger spatial scales (e.g., Cloyed et al. 2025).

We did not include depth or distance to coast as predictors because our study area was already restricted to waters ≤ 10 m, making depth redundant and potentially circular. Moreover, both variables are distal proxies of shallow nearshore habitats and could mask the contribution of ecologically direct predictors, such as seagrass presence and distance to freshwater springs, which represent essential requirements for manatees. Accordingly, we prioritized proximal variables with clear biological relevance, following recommendations that emphasized the use of direct ecological drivers over generic proxies to avoid obscuring underlying processes (Austin 2002; Elith and Leathwick 2009).

All data layers were standardized to a UTM 24S coordinate system with a resolution of 463 × 463 m (15 arc-second grid) and converted to ASCII file format, as required by MaxEnt for analysis (Figures S2–S6).

2.4 | Habitat Suitability Modeling

To investigate the environmental variables influencing manatee presence and to identify suitable habitats for the species in the study area, we used MaxEnt version 3.3.4 for maximum entropy modeling of habitat use (Phillips et al. 2006), implemented through the *maxent* function in the dismo package in R (version 1.3-16; Hijmans et al. 2017). MaxEnt is a widely used tool for species distribution and habitat modeling and is recognized as one of the best-performing algorithms in terms of predictive ability. It is particularly effective for presence-only data, outperforming many established modeling methods in predictive power (Valavi et al. 2021).

MaxEnt was run using 10,000 random background points, 500 iterations, linear and quadratic feature classes, a regularization multiplier of 2 to reduce overfitting (Radosavljevic and Anderson 2013), and a logistic output. We evaluated model performance using K-fold cross-validation. For each thinning scenario, we selected the largest number of folds that still retained at least 8–10 test presences per fold, with a maximum of 10 folds. The final number of folds used for each region is shown in Table 3, along with the effective number of presence records (Nef) retained after preprocessing and the number of test presences per fold.

Model selection followed a multi-criteria approach. Candidate models were compared using the continuous Boyce index (CBI) (Hirzel et al. 2006), AUC from cross-validation test data, omission rate (OR) at the maximum test sensitivity–specificity threshold (tMSS), and ΔAUC as an indicator of overfitting. The Boyce index, calculated in R using the function *ecospat.boyce* from the package *ecospat* (Broennimann et al. 2026), was used as the primary metric of predictive consistency because it evaluates the ability of the model to correctly rank habitat suitability using presence-only data. The index was computed using 10 suitability classes (nclass = 10), providing a stable assessment of predictive consistency for the available sample size.

In contrast to the CBI, AUC has recognized limitations when applied to presence-only models. It is sensitive to the spatial extent and composition of the background area (Jiménez-Valverde 2011;

TABLE 2 | Environmental variables used in the habitat suitability models for American manatees in the Potiguar Basin.

Variable	Rational	Unit	Source	Derivation
Distance to freshwater springs	Resource	Meters	Aquasis (2006); Normande et al. (2026)	Euclidian distance, ArcGIS Pro 3.2.0
Seagrass presence	Resource	Presence-Absence (Probability of Presence)	Based on Deeks, Katrina, et al. (2024) shapefile	Polygon to Raster ArcGIS Pro 3.2.0
Distance to river mouth	Potential freshwater and food (saltmarsh plant and mangrove) resources	Meters	This study. River mouth identified using Google Earth	Euclidian distance tool, ArcGIS Pro 3.2.0
Mean sea water velocity at the surface	Proxy to calm waters	Meters per second	Bio-Oracle (Assis et al. 2024)	Resample tool ArCGIS 3.2.0
Accumulated Human impact	Anthropogenic actions can act as stressors	Index	Magris et al. (2021) shapefile	Polygon to Raster ArcGIS Pro 3.2.0

Note: The table shows the ecological rationale for inclusion, measurement units, data sources, and procedures for derivation in ArcGIS.

TABLE 3 | Comparison of MaxEnt model performance and fit under alternative spatial thinning scenarios applied to telemetry data.

Thinning	Ntot	Ntel	Nsig	K-fold	Nef	Ntrain	Ntest	AUC train	AUC test	ΔAUC	Reg train gain	Test gain	OR	Test Max TSS	CBI
1×1	278	135	143	10	96	84	12	0.979	0.977	0.002	2.76	2.93	0.02	0.16	0.943
2×2	202	59	143	5	44	35.2	8.8	0.979	0.9724	0.0066	2.656	2.86	0.04	0.19	0.886
3×3	193	50	143	5	41	32.8	8.2	0.975	0.968	0.007	2.597	2.858	0.05	0.18	0.809
4×4	173	30	143	4	29	21.75	7.25	0.970	0.968	0.002	2.351	2.635	0.04	0.15	0.94
5×5	173	30	143	3	24	16	8	0.974	0.962	0.012	2.489	2.669	0.08	0.25	0.928

Note: Model evaluation metrics include training and test AUC, ΔAUC (difference between training and test AUC), regularized training gain, test gain, omission rate (OR) at the maximum sensitivity–specificity threshold, maximum TSS threshold value, and continuous Boyce index (CBI).

Abbreviations: K-fold = number of cross-validation folds; Nef = effective number of presence records used by MaxEnt preprocessing; Nsig = number of sighting records; Ntel = number of retained telemetry records after filtering; Ntot = total number of presence records (telemetry + sightings); Ntrain and Ntest = average number of training and test presences per fold.

Peterson et al. 2008), may yield inflated values when environmental gradients are broad (Jiménez-Valverde 2011), and evaluates discrimination rather than ecological calibration (Lobo et al. 2007). Moreover, AUC does not directly assess whether presences occur in areas predicted as highly suitable along the suitability gradient (Lobo et al. 2007). Therefore, CBI was considered more appropriate as the primary performance metric in this study, while AUC was retained as a complementary measure of overall discrimination ability.

To assess the relative influence of environmental predictors, we examined permutation importance and jackknife analyses in MaxEnt. Permutation importance reflects the decrease in model performance when the values of a given predictor are randomly permuted, indicating the model's dependence on that variable in the context of all predictors. Jackknife analyses were used to evaluate the unique contribution of each predictor to model gain by comparing models fitted with each variable in isolation and with each variable omitted. In MaxEnt, gain is a measure of how much better the model fits the data compared to a random distribution of presence points across the study area.

MaxEnt output was visualized as a gradient map showing the probability of manatee presence, ranging from 0% to 100% in ArcGIS Pro 3.5.2 2025. This gradient map was further converted into a binary map to delineate suitable and unsuitable habitats. The threshold for suitable habitat was defined using the MaxTSS, reported as the most effective thresholding method (Liu et al. 2013).

The absolute value of the difference between training AUC and test AUC was also calculated to assess the degree of overfitting in the models (Warren and Seifert 2011).

2.5 | Expert Evaluation

In addition to quantitative performance metrics, the final habitat suitability map was qualitatively evaluated by experienced regional manatee specialists with long-term field knowledge of the study area. Experts reviewed the spatial distribution of predicted suitable habitats and assessed their concordance with known areas of manatee occurrence and habitat use. This expert-based evaluation was used to assess ecological plausibility rather than to quantitatively recalibrate model outputs.

3 | Results

The Pearson correlation analysis revealed that most variables had low to moderate correlations that fell below the threshold of $|r| < 0.75$ –and were therefore acceptable for inclusion in the Maxent model. Models based on the 1×1 and 4×4 grid scenarios yielded highly comparable evaluation metrics (AUCtest, ΔAUC, and Boyce), suggesting limited sensitivity of model performance to the level of spatial thinning applied (Table 3). However, the stronger thinning in the 4×4 scenario substantially reduced the number of retained telemetry records (Nef ≈ 29), limiting cross-validation to four folds in order to maintain an adequate number of test records per replicate. This resulted in greater variability and discretization in threshold-dependent metrics. Given the equivalent predictive performance and the more stable cross-validation framework afforded by the larger sample size, we retained the 1 × 1 grid model as the primary model for subsequent analyses.

For the selected model, permutation importance and jackknife analyses consistently identified distance to freshwater springs as the dominant predictor of habitat suitability (Figure 2; Table 4). This variable exhibited the highest permutation importance (92.2%) and the greatest standalone regularized training gain (2.54). When omitted from the model, it produced the largest reduction in training gain ($\Delta = 1.1$), indicating both strong independent explanatory power and substantial unique contribution to overall model performance.

Seagrass presence showed comparatively low permutation importance (2.9%) but yielded moderate to high standalone gain (1.44; Table 4). The reduction in gain when removed from the model was small ($\Delta = 0.11$), suggesting that although seagrass availability contains relevant predictive information, part of its explanatory signal overlaps with the broader environmental gradient associated with proximity to freshwater springs.

Distance to river mouths, surface current velocity, and accumulated human impact exhibited low permutation importance and low standalone gain values (Table 4), and removing them reduced the model gain marginally ($\Delta \leq 0.04$). These predictors therefore contributed comparatively little independent explanatory power to regional habitat suitability patterns.

The response curve for "Distance to Springs" revealed a strong negative relationship with the predicted probability of manatee presence (Figure 3A). Predicted suitability was higher near freshwater springs but declined sharply between around 4–8 km. Beyond ~10 km from the nearest spring, the probability of presence dropped substantially and gradually stabilized at lower values with increasing distance. This pattern indicates a strong spatial association between manatee occurrence and proximity to submarine freshwater springs. The narrow confidence intervals further indicate a high level of certainty in this relationship across model replicates.

The response curve for seagrass presence indicated a positive but weaker non-linear relationship with predicted manatee occurrence (Figure 3B). Predicted suitability increased as the probability

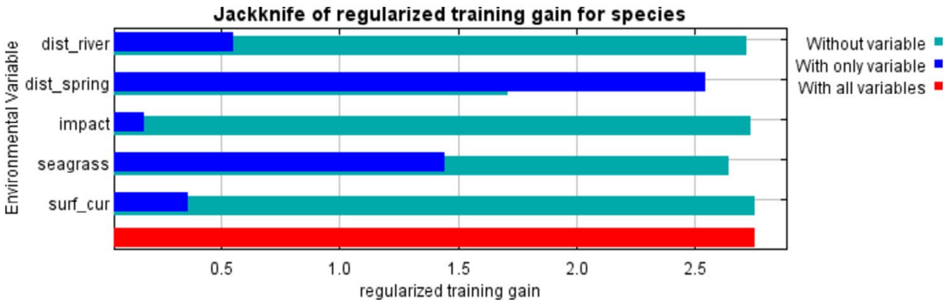

FIGURE 2 | Jackknife test for regularized training gain of individual explanatory variable importance (blue bars) relative to all variables (red bar) for the full Maxent model.

TABLE 4 | Relative importance of environmental predictors in the selected MaxEnt model.

Variable	Percent contribution	Permutation importance	Regularize training gain (alone)	Gain drop (removed)	Interpretation
Distance to freshwater springs	76.3%	92.2%	2.54	1.05	Primary structural driver; high independent information
Seagrass presence	17.4%	2.9%	1.44	0.11	Secondary predictor; partial informational potential redundancy with springs
Distance to river mouth	1.5%	3.1%	0.55	0.04	Minor but independent gradient
Mean sea water velocity at the surface	2.7%	0.6%	0.36	0.003	Weak regional effect; possible local modulation
Accumulated human impact	2.1%	1.3%	0.17	0.02	Limited independent predictive power

Note: Percent contribution reflects the increase in regularized training gain attributed to each variable during model fitting. Permutation importance measures the decrease in model performance when values of a predictor are randomly permuted, indicating model dependence on that variable. Regularized training gain (alone) represents model gain when each predictor is used in isolation, whereas gain drop (removed) indicates the reduction in model gain when that variable is excluded from the full model.

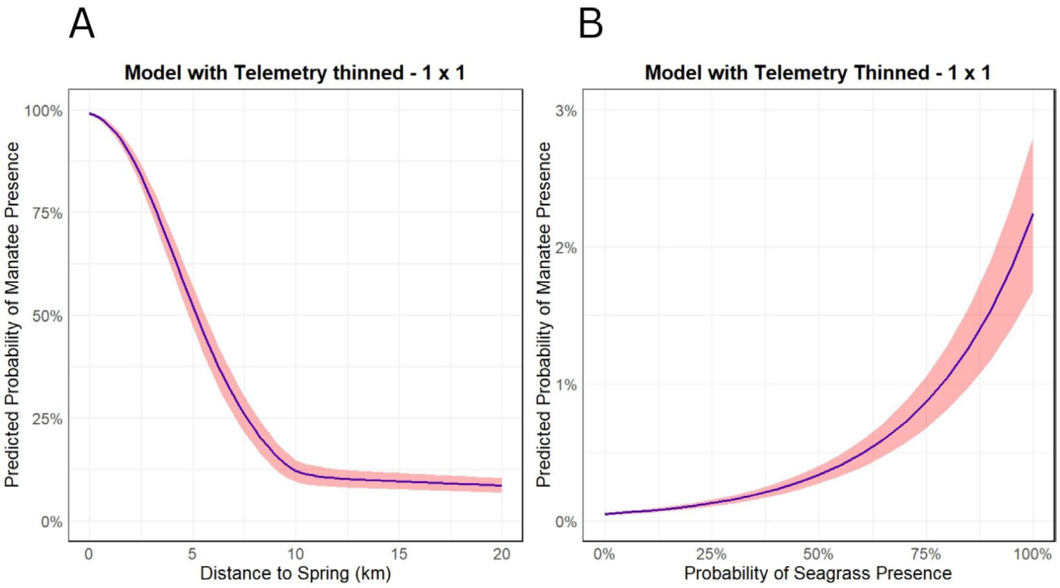

FIGURE 3 | Response curves showing the predicted probability of manatee presence in relation to key variables: (A) Distance to submarine freshwater springs, (B) probability of seagrass presence. Curves represent mean predictions across four model replicates, with shaded areas indicating standard deviation.

of seagrass presence increased, reaching a maximum of approximately 2%–3% when seagrass probability approached 100%. While suitability increased along the gradient of seagrass probability, confidence intervals widened at higher values, indicating increased uncertainty in areas with high predicted seagrass presence.

The highest likelihood of manatee occurrence is concentrated in the central portion of the study area (Figure 4A), especially near the municipalities of Icapuí and Aracati (Ceará). This contrasts considerably from most of the study area that had low probabilities of occurrence. Only 301 km^2 (4%) of the studied area was classified as suitable habitat for manatees after applying the max TSS threshold (0.16) (Figure 4B). A large and continuous stretch of suitable habitat was identified from Fontainhas to Tremembé, in Icapuí, covering all the Cajuais Bank (Figure 4B). In contrast, a fragmented area was identified near the mouth of the Jaguaribe River. In the state of Rio Grande do Norte, a broad but fragmented suitable zone extends from Gado Bravo (Grossos) to São Joseé Beach, followed by a wide unsuitable area, and then another fragmented suitable stretch off the coast of Porto do Mangue. The entire area extending westward from the Jaguaribe River to Aquiraz was classified as unsuitable, as well as the area from Diogo Lopes to Cajueiro.

The binary suitability map was evaluated by regional manatee specialists familiar with the study area. Experts generally agreed with the spatial distribution of predicted suitable habitats; however, they indicated that some areas classified as unsuitable may still be used by manatees.

4 | Discussion

The habitat used by the fully marine American manatee population that inhabits Brazil's semi-arid coast appears to be unique within the global range of habitats used by the species. Unlike other populations of *T. manatus*, which rely mainly on rivers as a regular source of freshwater (e.g., Corona-Figueroa et al. 2020; Olivera-Gómez and Mellink 2005), manatees in the Potiguar Basin have been reported occupying exclusively marine waters year-round, with no documented use of estuaries in recent years (Choi-Lima et al. 2017; Meirelles et al. 2024).

4.1 | Environmental Drivers of Habitat Suitability

Our habitat suitability model reveals that manatee presence in the Potiguar Basin is strongly associated with proximity to submarine freshwater springs. Seagrass presence also contributed to habitat suitability, but its effect was secondary compared to the strong influence of freshwater availability. In contrast, distance to river mouths was not an important predictor of habitat use in the Potiguar Basin, reinforcing the notion that this population probably does not depend on estuarine food and freshwater.

Historical records of manatee presence within estuaries in our study region (Choi-Lima et al. 2017) suggest that estuaries may once have played a more prominent role in their seasonal habitat use. However, the increasing duration and intensity of hypersaline conditions in recent decades may have reduced the suitability of local estuaries as reliable freshwater habitat.

In contrast, seasonal use of estuaries continues along the nearby Piauí coast, also part of Brazil's semi-arid coast, where manatees still use a large estuarine complex that has lower salinity levels during the rainy season. Habitat use of the Piauí coast varies seasonally with freshwater availability, whereby individuals concentrate in the estuary during the rainy season and move to marine areas near submarine freshwater springs during the dry season, when the estuary becomes hypersaline (Favero et al. 2020).

Seagrass presence was identified by our model as the second most important variable explaining manatee presence, underscoring the ecological value of this food source—an importance

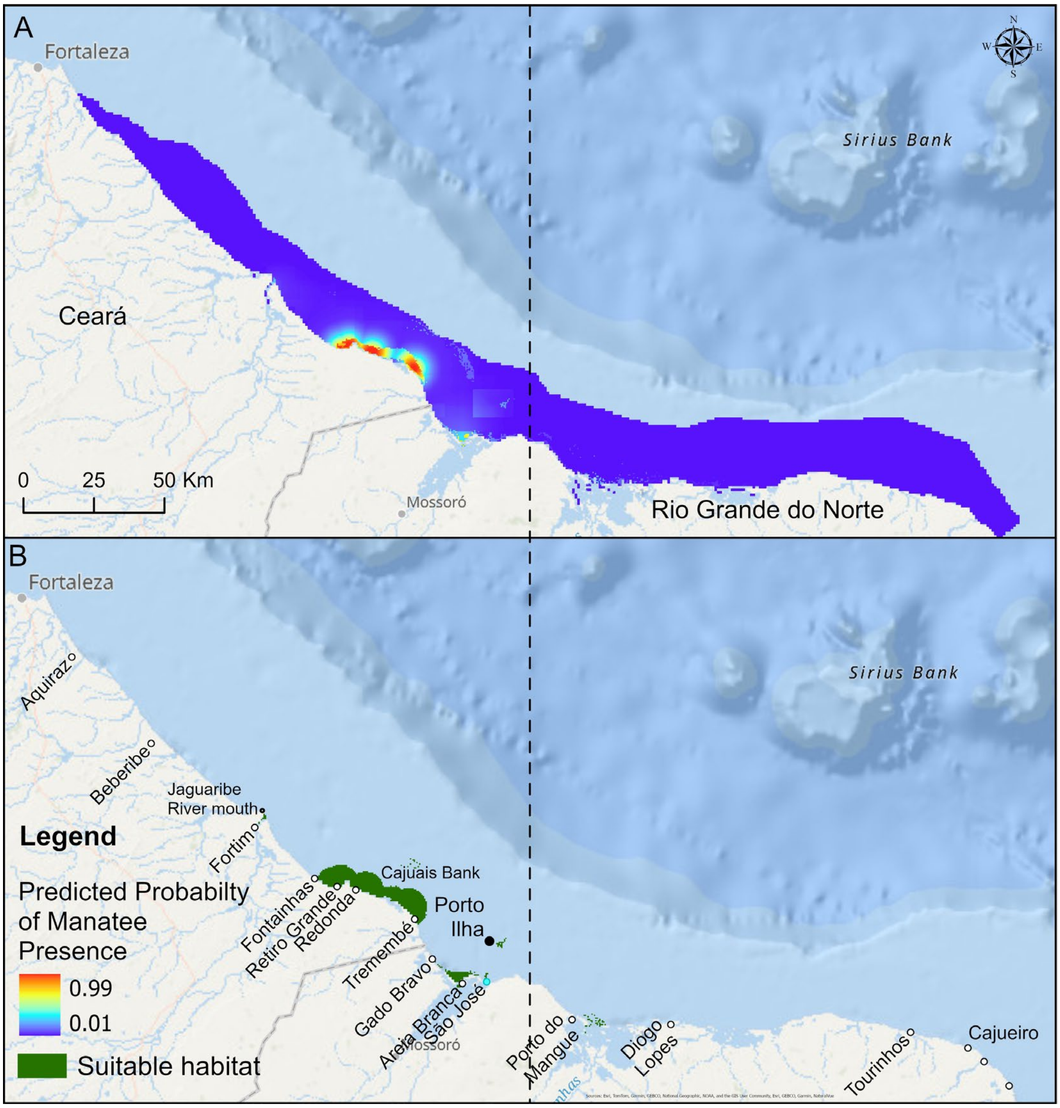

FIGURE 4 | (A) Predicted probability of manatee presence generated by the MaxEnt model, with warmer colors indicating higher suitability. (B) Binary habitat suitability map highlighting areas classified as suitable habitat (in green), based on the Maximum Sensitivity plus Specificity threshold. The dashed vertical line is included to facilitate visual comparison between the two panels.

well documented in previous diet studies (Carvalho 2019; Ciotti 2012; Vasconcelos 2013). In contrast, no environmental proxies related to other potential food items—such as macroalgae, mangrove, or saltmarsh plants—emerged as significant predictors of habitat use, consistent with prior dietary findings. The absence of mangrove and saltmarsh plant predictors is ecologically consistent with this population not using estuarine habitats where these plants grow (Choi-Lima et al. 2017). Macroalgae, although widely distributed in the Potiguar Basin, contribute minimally to their diet (3%) (Ciotti 2012), likely due to the greater availability and higher nutritional value of seagrass meadows compared to macroalgal resources (Meirelles et al. 2018).

4.2 | Human Pressures and Emerging Threats

In our model, accumulated human impact showed no evidence of independently structuring manatee occurrence, indicating no detectable pattern of habitat use along the regional impact gradient. However, human pressures are dynamic, and future changes in cumulative impact levels over time could alter habitat quality and subsequently influence habitat use. Intensification of impacts within currently used areas could lead to avoidance or reduced occupancy, potentially strengthening links between occurrence and human impact. Conversely, effective mitigation could maintain or even increase use of areas experiencing anthropogenic pressures.

In the study region, there is already a port infrastructure linked to salt production in the municipality of Areia Branca, Rio Grande do Norte, including an offshore terminal (*Porto Ilha*) located 13 km from the coast (Figure 4B). This presence highlights potential conservation challenges, as port operations may increase exposure to vessel traffic, underwater noise, and other disturbances known to affect manatees (Rycyk et al. 2018), raising concerns regarding cumulative impacts in areas that remain ecologically valuable. From a management perspective, these findings underscore the relevance of explicitly incorporating manatee presence, habitat use, and impact monitoring into environmental licensing and permitting processes for coastal and offshore infrastructure, as is routinely required for oil and gas developments in Brazil (Vilardo et al. 2020).

Looking forward, the planned expansion of offshore activities along the northeastern Brazilian coast—including proposed offshore wind energy projects—reinforces the need for proactive spatial planning. Recent analyses of offshore wind energy development in Brazil further reinforce this concern, as spatial assessments reveal multiple licensing requests for the implementation of offshore wind farms concentrated in shallow coastal waters of the Potiguar Basin, particularly along the coast of Rio Grande do Norte (Gorayeb et al. 2024). This pattern underscores the importance of explicitly incorporating manatee occurrence, habitat use, and cumulative impact assessments into environmental licensing processes, as well as defining spatial and temporal exclusion zones for sensitive species, similar to the spatial and temporal exclusion measures already established for seismic surveys and, in some cases, applied to other phases of oil and gas activities (Vilardo et al. 2020). Such measures will be essential to minimize conflicts between offshore development and the persistence of critical manatee habitats.

The fragmented pattern of suitable habitat predicted by our model largely mirrors the patchy distribution of seagrass meadows in our study area, which is especially fragmented outside the Cajuais Bank (Figure 4B), where seagrass forms more extensive and continuous meadows (Deeks, Magalhães, et al. 2024). However, manatees also traverse areas classified by the model as unsuitable to move between suitable patches. Thus, zones of lower suitability may still play a role in maintaining connectivity, acting as a matrix that facilitates movements between critical foraging sites and freshwater sources. This limitation should be considered when interpreting our results and applying them in conservation planning, ensuring that priority areas include not only highly suitable habitat cores, but also the corridors that connect them (see Zacarias and Loyola 2018).

4.3 | Model Evaluation and Data Limitations

Expert evaluation of the binary suitability map revealed partial agreement with the predicted classification. While specialists broadly supported the spatial distribution of highly suitable areas, some locations classified as unsuitable were thought to be used occasionally by manatees. This discrepancy may stem from using a relatively conservative threshold, which prioritizes minimizing commission errors and is commonly preferred in conservation-oriented applications (Liu et al. 2013). Importantly, the expert review of model predictions was not intended as a statistical validation step—model performance had already been assessed using quantitative metrics—but rather as an ecological plausibility check. Incorporating regional expertise provided an additional layer of interpretation, helping to verify whether spatial predictions align with long-term field knowledge and ecological understanding of the system (e.g., Tardin et al. 2025).

Although our model identified clear environmental drivers of habitat suitability, some considerations regarding the structure of the occurrence dataset are warranted. Telemetry locations were obtained for individuals captured and released in Ceará, with only one male regularly extending movements into Rio Grande do Norte, whereas females exhibited more restricted displacement patterns (Normande et al. 2024). This imbalance in individual movement patterns may have influenced the spatial distribution of high-resolution occurrence data, potentially increasing representation of environmental conditions in the Ceará sector relative to Rio Grande do Norte.

Including sighting records from Rio Grande do Norte partially offsets the limitation of uneven spatial representation of occurrence data caused by telemetry tracks being concentrated in Ceará. These additional sighting records provided independent evidence of manatee presence across the broader study area. Still, expanding telemetry efforts within Rio Grande do Norte would ultimately yield a more balanced depiction of habitat use and refine suitability estimates, particularly in coastal segments that remain under-sampled.

In addition, traditional ecological knowledge (TEK) from coastal communities of Rio Grande do Norte and Ceará provides further contextual support for the predicted spatial pattern. TEK reports indicate an absence of recent manatee records west of Fortim and in portions east of Diogo Lopes (Choi-Lima et al. 2017)—areas that our model also identified as having low habitat suitability.

4.4 | Broader Context and Conservation Implications

Most habitat suitability studies for the American manatee have focused on mixed environments, such as freshwater-estuarine or marine-estuarine systems. To our knowledge, the only study centered on a fully marine setting examined a relatively small portion of the species' broader range in Belize (Bevan 2023), where manatees use both marine and estuarine habitats (Castelblanco-Martínez et al. 2013). Consequently, direct comparisons with our study are of limited value. More broadly, research that includes marine environments consistently identifies low salinity or proximity to freshwater sources—such as rivers, submarine springs, and sink holes—as strong predictors of manatee presence (Cloyed et al. 2025; Deeks, Katrina, et al. 2024; Favero et al. 2020; Gagnon et al. 2026; Olivera-Gómez and Mellink 2005), underscoring the manatees' physiological dependence on freshwater.

In the same coastal system of our study, habitat use has also been investigated using resource selection analyses at finer spatial scales (Normande et al. 2026). At this local scale, freshwater springs and seagrass meadows were not identified as significant predictors, with human impact emerging as the only consistent effect. These differences likely reflect the contrasting spatial scales and analytical frameworks of the two approaches whereby resource selection functions describe within-home-range processes, and habitat suitability models capture broader environmental gradients across the studied coastal region.

Our findings have important conservation implications for this fully marine population of manatees. The persistence of critical habitat features—particularly submarine freshwater springs and seagrass meadows—highlights the need to recognize and prioritize these resources in conservation planning. These groundwater-fed upwellings from coastal aquifers emerge from the continental shelf where hydrostatic pressure discharges into the sea (Meireles 2014). However, these aquifers are increasingly threatened by saltwater intrusion and sewage contamination, as most towns lack basic sanitation infrastructure and rely on rudimentary cesspits (Meireles 2016). Moreover, climate change projections for the region indicate that longer and more intense droughts will reduce groundwater recharge (Dias et al. 2016; Soares et al. 2021) and further compromise the flow and quality of submarine freshwater discharge—the primary freshwater source available to manatees in this hypersaline system.

Equally concerning as the loss of freshwater springs is the risk of seagrass decline. Reduced seagrass availability could have severe consequences for manatees in the Potiguar Basin, given their apparent dietary specialization and the limited nutritional contribution of alternative food sources. Evidence from Florida's Indian River Lagoon shows that shifting to a more macroalgae-dominated diet following widespread seagrass loss may not sustain long-term manatee health (Allen et al. 2022). Since the onset of seagrass die-offs, this Florida population has experienced increased mortality and deteriorating body condition, raising concerns about the energetic and nutritional adequacy of macroalgae (Allen et al. 2024). Although macroalgae may form a substantial part of the diet of some manatee populations (Borges et al. 2008) due possibly to greater availability, its nutritional value is generally lower compared to seagrasses such as shoal grass (Rodrigues et al. 2021).

Our study aimed to identify the environmental drivers shaping habitat suitability for Brazil's fully marine population of manatees in the Potiguar Basin. Our results highlight the central role of shallow coastal environments associated with submarine freshwater springs and seagrass meadows in supporting manatee presence, even within landscapes increasingly influenced by human activities. These findings refine understanding of the ecological constraints faced by this unique population and emphasize the importance of safeguarding the key resources that sustain it. Importantly, while habitat suitability represents a fundamental ecological component, future research should integrate these results with connectivity analyses, movement corridors, cumulative impacts, and socio-environmental factors to support comprehensive conservation prioritization and spatial planning in this rapidly changing coastal region.

Author Contributions

L. von Fersen: writing – review and editing. **K. F. Choi:** methodology, validation, writing – review and editing, data curation. **I. C. Normande:** methodology, validation, writing – review and editing, data curation. **V. L. Carvalho:** data curation, validation. **J. C. G. Borges:** validation, writing – review and editing, data curation. **M. D. O. Alves:** methodology, validation, writing – review and editing, data curation. **A. C. O. Meirelles:** conceptualization, investigation, funding acquisition, writing – original draft, methodology, validation, visualization, writing – review and editing, formal analysis, project administration, data curation. **Andrew W. Trites:** funding acquisition, writing – review and editing, supervision.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Research data are not shared.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Pearson correlation matrix showing relationships among environmental variables used in the habitat models. Values represent pairwise correlation coefficients between predictors, with color intensity indicating the strength and direction of the correlation. **Figure S2:** Map for the Distance to river mouth explanatory variable, used to model the American manatee habitat in the Potiguar Basin. **Figure S3:** Map for the Cumulative Impact Index explanatory variable, used to model the American manatee habitat in the Potiguar Basin. **Figure S4:** Map for the Distance to freshwater submarine spring explanatory variable, used to model the American manatee habitat in the Potiguar Basin. **Figure S5:** Map for the Surface current velocity explanatory variable, used to model the American manatee habitat in the Potiguar Basin. **Figure S6:** Map for the Seagrass presence explanatory variable, used to model the American manatee habitat in the Potiguar Basin. **Data S1:** mms70194-sup-0002-Supinfo1.docx.