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Ecological Niche Modeling of Three Species of *Stenella* Dolphins in the Caribbean Basin, With Application to the Seaflower Biosphere Reserve

Dalia C. Barragán-Barrera[1,2]*, Karina Bohrer do Amaral[3]*,
Paula Alejandra Chávez-Carreño[4], Nohelia Farías-Curtidor[1], Rocío Lancheros-Neva[1,5],
Natalia Botero-Acosta[1], Paula Bueno[6], Ignacio Benites Moreno[3,7],
Jaime Bolaños-Jiménez[8,9], Laurent Bouveret[10], Delma Nataly Castelblanco-Martínez[11,12],
Jolanda A. Luksenburg[13,14], Julie Mellinger[10], Roosevelt Mesa-Gutiérrez[15],
Benjamin de Montgolfier[16], Eric A. Ramos[12,17], Vincent Ridoux[18] and
Daniel M. Palacios[19]*

[1] Fundación Macuáticos Colombia, Medellín, Colombia, [2] Laboratorio de Ecología Molecular de Vertebrados Acuáticos, Department of Biological Sciences, Universidad de los Andes, Bogotá, Colombia, [3] Laboratório de Sistemática e Ecologia de Aves e Mamíferos Marinhos, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil, [4] Independent Researcher, La Paz, Mexico, [5] Parques Nacionales Naturales de Colombia, Bogotá, Colombia, [6] WWF Colombia, Bogotá, Colombia, [7] Centro de Estudos Costeiros, Limnológicos e Marinhos, Universidade Federal do Rio Grande do Sul, Imbé, Brazil, [8] Asociación Civil Sea Vida, Aragua, Venezuela, [9] Instituto de Ciencias Marinas y Pesquerías, Universidad Veracruzana, Veracruz, Mexico, [10] Observatoire des Mammifères Marins de l'Archipel Guadeloupéen, Archipelago's Guadeloupe, France, [11] Consejo Nacional de Ciencia y Tecnología, University of Quintana Roo, Chetumal, Mexico, [12] Fundación Internacional para la Naturaleza y la Sostenibilidad, Chetumal, Mexico, [13] Institute of Environmental Sciences, Leiden University, Leiden, Netherlands, [14] Department of Environmental Science and Policy, George Mason University, Fairfax, VA, United States, [15] Duke Marine Laboratory, Nicholas School of the Environment, Duke University, Durham, NC, United States, [16] Aquasearch, Sainte-Luce, France, [17] The Graduate Center, City University of New York, New York, NY, United States, [18] Observatoire PELAGIS, Université de La Rochelle, La Rochelle, France, [19] Marine Mammal Institute and Department of Fisheries and Wildlife, Oregon State University, Newport, OR, United States

Dolphins of the genus *Stenella* occur in pelagic waters of both tropical and warm-temperate oceans. Three species, the Atlantic spotted dolphin (*Stenella frontalis*), the pantropical spotted dolphin (*S. attenuata*), and the spinner dolphin (*S. longirostris*) are abundant worldwide, but in the Caribbean Basin they have been poorly studied and information on their distribution patterns is scarce. Specifically, in Colombia's remote Seaflower Biosphere Reserve (SFBR) *S. attenuata* has been reported occasionally, but *S. frontalis* and *S. longirostris* have never been recorded before. To address this information gap, an ecological niche modeling approach was used to determine the potential distribution patterns of these three dolphin species in the region. Records of these species for the Caribbean Basin were compiled, including both published and unpublished data. Environmental information, including bathymetry, bathymetric slope, distance to shore, sea surface temperature, sea surface salinity, and chlorophyll-*a* concentration was gathered from public databases (MARSPEC and Bio-ORACLE) in raster format. The maximum entropy algorithm (Maxent) for modeling species' geographic distributions with presence-only data was used. After filtering the data, 210 records of *S. attenuata*, 204 of *S. frontalis*, and 80 of *S. longirostris* were used to run models. The best configuration for each model was chosen based on the ΔAICc criterion. For all three species, the final ecological niche models returned AUC

test values higher than 0.8, indicating satisfactory model performance. The resulting potential distribution maps suggested that areas closest to continental shorelines of the Caribbean Basin and surrounding islands had the highest environmental suitability for all species (>70%). All models reported high environmental suitability for *S. attenuata* and *S. longirostris* in the SFBR, mainly in the southernmost part surrounding San Andrés and Providence Archipelago. Assessment of niche overlap from the predictions of species distributions using the similarity statistic and pairwise map overlap indicated that *S. frontalis* and *S. longirostris* had niches slightly more similar in comparison to *S. attenuata*. As this was a first effort to fill a gap in our understanding of the distribution of species in the genus *Stenella* in the Caribbean Basin, further studies are necessary using both niche modeling and biological/ecological approaches.

INTRODUCTION

The ocean comprises 70% of the planet and offers a wide range of habitats to marine life (e.g., Spalding et al., 2012; Kelley et al., 2016). These different habitats are characterized by gradients in sea surface temperature (SST), sea surface salinity (SSS), productivity, and topography at both broad and local scales (Redfern et al., 2006), playing an important role to explain distribution patterns of marine top predators such as cetaceans (e.g., Baumgartner et al., 2001; Palacios et al., 2013b). Dolphins of the genus *Stenella* (Gray, 1866) are common in tropical, subtropical, and temperate waters worldwide. Because of such wide distribution patterns, they are often considered "umbrella species," since any conservation efforts made on their behalf benefit many other species within their habitat (Jefferson et al., 2008).

Although the taxonomy of *Stenella* remained unclear until the 1980s, the five species that make up the genus are now well characterized. The genus is considered a non-monophyletic assemblage (see Perrin et al., 2013), with some species being more related to *Tursiops* (Leduc et al., 1999). While the *Stenella* species have great dispersal capacity, they exhibit significant distribution changes in response to seasonal variation in oceanographic conditions (Reilly, 1990; Moreno et al., 2005). Additionally, some species within the genus are considered sympatric throughout their distribution, although at an individual level they appear to have distinct environmental requirements at regional scales (e.g., Baumgartner et al., 2001; Davis et al., 2002; do Amaral et al., 2015).

The Atlantic spotted dolphin (*S. frontalis*), endemic to the Atlantic Ocean, is distributed mainly in areas closer to continental shelves and surrounding islands (Perrin et al., 1987; Davis et al., 1998; do Amaral et al., 2015). The pantropical spotted dolphin (*S. attenuata*) and the spinner dolphin (*S. longirostris*) are more widely distributed in the Atlantic, Indian, and Pacific Oceans (Jefferson et al., 2008), and appear to have similar patterns of habitat use that favor their presence over deeper waters (Davis et al., 1998, 2002; Baumgartner et al., 2001; do Amaral et al., 2015). Although these three species have been previously reported in the Caribbean Basin (e.g.,

Caldwell et al., 1971; Mignucci-Giannoni, 1998; Pardo et al., 2009; Palacios et al., 2013b; Niño-Torres et al., 2015; Ramos et al., 2016), little is known about their habitat preferences and spatial distribution in coastal or oceanic areas. Hence, it is important to identify areas where these species are likely to be found in order to direct research and improve management measures.

Particularly in Colombia's Caribbean Sea, cetacean research has been limited, with most studies focusing on specific coastal mainland locations, including Santa Marta (Pardo and Palacios, 2006; Fraija et al., 2009; Pardo et al., 2009), Bay of Cispatá (García and Trujillo, 2004), Gulf of Morrosquillo (Palacios et al., 2013b), and La Guajira (Combatt and González, 2007; Palacios et al., 2012; Farías-Curtidor et al., 2017). To date, almost no research effort has been conducted in the remote oceanic region surrounding the Archipelago of San Andrés, Providencia and Santa Catalina (Pardo et al., 2009; Palacios et al., 2013b). Located in this region, the Seaflower Biosphere Reserve (SFBR) is one of the largest marine reserves in the western hemisphere, containing the most extensive open-ocean coral reefs in the Caribbean Sea (Mow et al., 2007; Coralina-Invemar, 2012). This unique marine ecosystem is highly biodiverse (Taylor et al., 2013) and may be of importance for cetaceans. However, given the remoteness of the region and the prevalence of windy conditions, the development of systematic visual surveys necessary to assess cetacean abundance and distribution has been logistically and financially challenging.

To date, at least 22 species of marine mammals have been confirmed to occur in the Colombian Caribbean, including 18 odontocetes (Palacios et al., 2013b). Within the SFBR, pantropical spotted dolphins, bottlenose dolphins (*Tursiops truncatus*), false killer whales (*Pseudorca crassidens*), and sperm whales (*Physeter macrocephalus*) are all confirmed species (Pardo et al., 2009; Barragán-Barrera et al., 2017). Stranding reports in the San Andrés Archipelago also indicate the presence of pygmy or dwarf sperm whales (*Kogia* sp.) (Palacios et al., 2013b) and Cuvier's beaked whales (*Ziphius cavirostris*) (Prieto-Rodríguez, 1988; Vidal, 1990). However, the area can potentially host several other species, including Atlantic spotted dolphins, spinner dolphins, striped dolphins (*S. coeruleoalba*), short-finned pilot whales

(*Globicephala macrorhynchus*), killer whales (*Orcinus orca*), and even humpback whales (*Megaptera novaeangliae*) (Pardo et al., 2009; Palacios et al., 2013b; Bolaños-Jiménez et al., 2014).

Ecological niche modeling is a widely used tool to predict cetaceans' distribution and understand the ecological precursors (Redfern et al., 2006; Gregr et al., 2013; Palacios et al., 2013a). These models can also be implemented to assess areas of high conservation priority and identify key areas for research on interactions between humans and wildlife (Bailey and Thompson, 2009). For the Caribbean Basin, the use of advanced geospatial analysis tools has the potential to improve the current comprehension of cetacean distribution patterns and the environmental factors influencing them. However, these analyses have never been conducted in the region, despite some studies being developed in the adjacent Gulf of Mexico (e.g., Davis et al., 1998, 2002; Baumgartner et al., 2001) and the Western South Atlantic Ocean (e.g., do Amaral et al., 2015). Since 2014, Colombia has been carrying out scientific cruises in the SFBR to assess the local biodiversity of the islands (Murillo, 2014). Despite cetaceans having been taken into account in these efforts, in practice the Colombian Program of Marine Fauna Observers has been the main source of this type of information in recent times (Palacios et al., 2013b). Research efforts could be optimized if uncertainty regarding cetacean occurrence and distribution in the Reserve is overcome.

With the aim of determining the potential distributions of spotted and spinner dolphins throughout the Caribbean Basin, and more specifically within the SFBR, we adopted an ecological niche modeling approach. Because absence data are generally not available for oceanic dolphins and the offshore limits of their distributions are unknown, we used a presence-only method to predict the potential distribution of these species (Robinson et al., 2017). The chosen method was maximum entropy (Phillips et al., 2006), which has been applied successfully on species with limited data (Wisz et al., 2008; Elith et al., 2011). Furthermore, this method has been successfully used with cetaceans (Derville et al., 2018), and has already been used to predict the potential distribution of *Stenella* species in the Western South Atlantic (do Amaral et al., 2015). We hypothesized that these species have different distribution patterns as a consequence of distinct environmental requirements, as has been found in adjacent regions such as the Gulf of Mexico and the Western South Atlantic. In addition to overcoming the prevailing information gaps, our results could contribute to the understanding of the effectiveness of the SFBR in protecting top predators such as dolphins, and to identify other areas that deserve protection throughout the Caribbean Basin.

MATERIALS AND METHODS

Study Area
The geographical extent of the models and the background sampling was restricted to the Caribbean Basin (59°24′W–89°21′W and 7°42′N–22°41′N). The Caribbean is a semi-enclosed tropical sea adjacent to the Atlantic Ocean (Müller-Karger et al., 1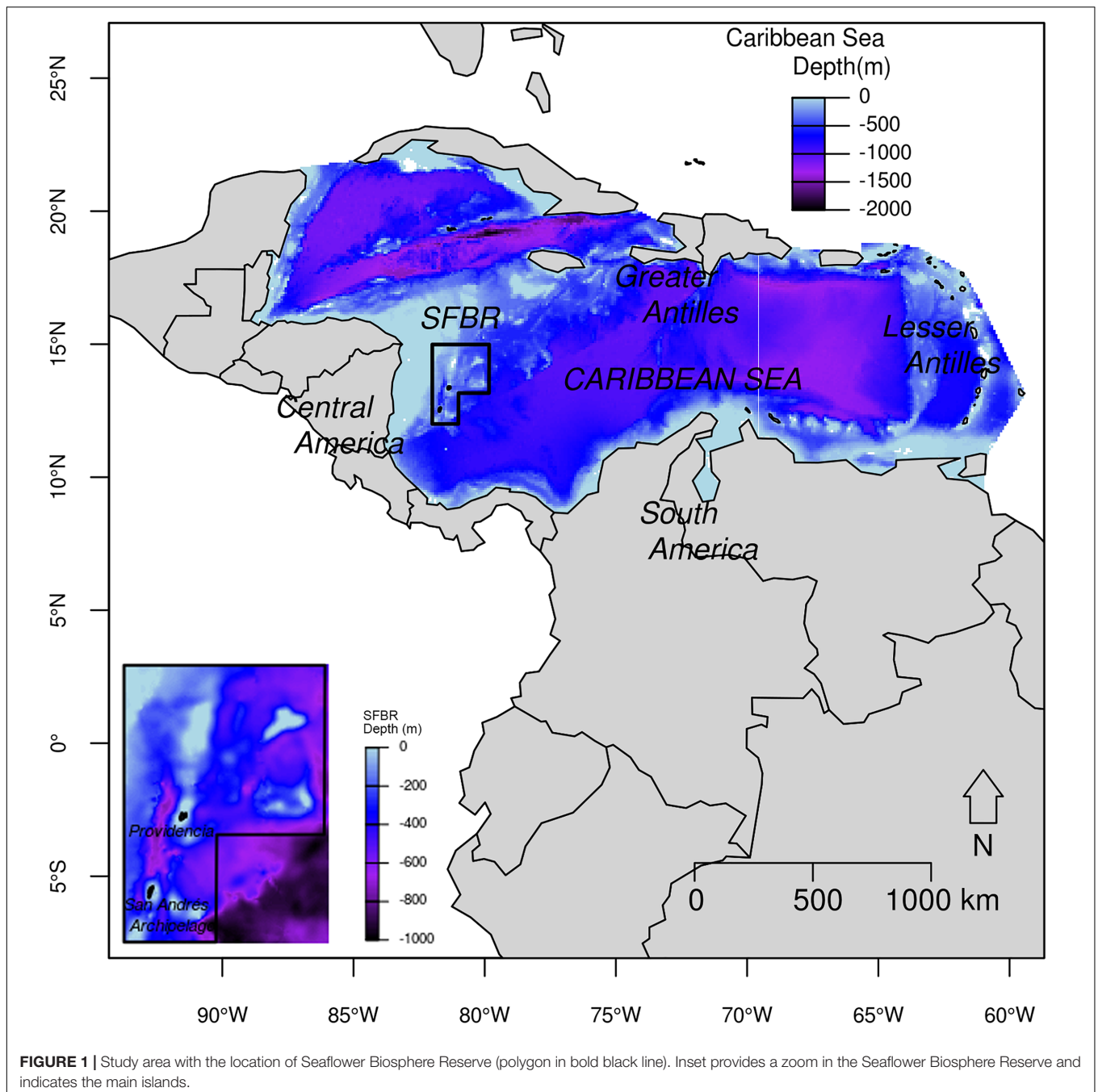989; Aguirre, 2014). Although the area is influenced by the discharge of the Amazon and Orinoco rivers, it is generally considered oligotrophic and homogeneous despite seasonal upwelling events (Müller-Karger et al., 1989; Criales-Hernández et al., 2006; Arévalo-Martínez and Franco-Herrera, 2008; Chollett et al., 2012; Rueda-Roa and Muller-Karger, 2013), and the influence of the warm Caribbean Current (Aguirre, 2014).

Within the Caribbean Basin, the SFBR is located in oceanic waters of the Colombian Exclusive Economic Zone (80°39′W–82°17′W and 11°56′N–13°55′N) (Coralina-Invemar, 2012) (**Figure 1**). The Reserve was created as the first Colombian Marine Protected Area and was declared as a UNESCO Biosphere Reserve in November 2000 (Taylor et al., 2013). It has an area of around 65,000 km^2 and encompasses the San Andrés, Providencia and Santa Catalina Archipelago (**Supplementary Figure S1**) (Taylor et al., 2013). The SFBR is a highly biodiverse region, containing more than 77% of the shallow coral reefs of Colombia, as well as other coastal/marine ecosystems such as atolls, beaches, sandy bottoms, mangroves, and seagrass beds (Coralina-Invemar, 2012; Taylor et al., 2013).

Environmental Data
Environmental layers used in the modeling were selected after reviewing previous cetacean niche modeling studies (e.g., Baumgartner et al., 2001; Cañadas et al., 2002; Davis et al., 2002; do Amaral et al., 2015; Tobeña et al., 2016; Gomez et al., 2017). The selected layers included both static and dynamic variables for all three species (**Table 1**). Dynamic variables used in this study included SST, chlorophyll-*a* concentration (Chl-a), diffuse attenuation (Da), and SSS. Static layers included bathymetry, slope and distance to shore (**Table 1**). Environmental layers representing SST, SSS and Chl-a were included as two different metrics: the annual mean and the annual range (the differences between annual maximum and minimum). For Da, only the annual mean was included because annual range was not available.

Raster layers of dynamic and static information data were gathered from the public database Bio-Oracle (Oceans Rasters for Analysis of Climate and Environment) (Tyberghein et al., 2012) and MARSPEC (Ocean Climate Layers from Marine Spatial Ecology) (Sbrocco and Barber, 2013). While the Bio-Oracle public database carried raster layers of Chl-a and Da at the 9.2 km resolution, the remaining layers were available in the MARSPEC public database at 1 km resolution. All layers were cropped to encompass the study area and adjusted to a common resolution of 9.2 km per grid cell using the raster package (Hijmans, 2017) in R 3.4.2 (R Core Team, 2018). The correlation among layers was investigated using the function pairs in the raster package. Only layers with correlation coefficient below 0.7 were included in the ecological niche models (Dormann et al., 2013) (**Supplementary Figure S2**). A principal component analysis (PCA) was performed to visualize the environmental heterogeneity across the study area using the rasterPCA function from Rstoolbox package (Leutner and Horning, 2016) (**Supplementary Figure S3**).

FIGURE 1 | Study area with the location of Seaflower Biosphere Reserve (polygon in bold black line). Inset provides a zoom in the Seaflower Biosphere Reserve and indicates the main islands.

Occurrence Data

Georeferenced sighting data for Atlantic spotted dolphins, pantropical spotted dolphins, and spinner dolphins occurring between 1981 and 2016 in the Caribbean Basin, were compiled from several sources: published records, unpublished data, and the Sistema de Información Ambiental Marina (SIAM[1]) operated by the Instituto de Investigaciones Marinas y Costeras (INVEMAR, Colombia's Marine and Coastal Research Institute). These occurrence data were collected through different seasons

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[1]http://siam.invemar.org.co

and years, during both systematic and opportunistic marine wildlife observations. Only confirmed sightings correctly identified at the species level as *Stenella* were included.

After scrutinizing, filtering, cleaning duplicate records and removing some of the bias by subsampling records (see Hijmans and Elith, 2017), a total of 494 records were included: 210 sightings of pantropical spotted dolphins, 204 Atlantic spotted dolphins, and 80 spinner dolphins (**Table 2** and **Figure 2**). The dataset used for this study is presence-only, meaning that absences (such as survey track lines) were not considered (Franklin, 2009). A subset of records (20%) was used as testing

TABLE 1 | List of environmental variables used in this study and their respective source, original grid resolution, and unit of measurement.

Environmental variables	Source	Unit	Original resolution
Bathymetry (depth of the seafloor)	MARSPEC	m	1 km
Distance to shore	MARSPEC	km	1 km
Bathymetric slope	MARSPEC	degrees	1 km
Mean annual chlorophyll-*a* concentration	Bio-Oracle	mg/m^3	9 km
Annual range in chlorophyll-*a* concentration	Bio-Oracle	mg/m^3	9 km
Mean annual diffuse attenuation	Bio-Oracle	m^{-1}	9 km
Mean annual sea surface salinity	MARSPEC	psu	1 km
Annual range in sea surface salinity	MARSPEC	psu	1 km
Mean annual sea surface temperature	MARSPEC	°C	1 km
Annual range in sea surface temperature	MARSPEC	°C	1 km

data as explained below, and the remaining was used as training data.

Ecological Niche Modeling

We used a presence-only approach to model the distribution of *Stenella* species in the Caribbean Basin. Specifically, we used the maximum entropy (Maxent) algorithm (Phillips et al., 2017) to model the potential distribution of the three species. Maxent estimates the geographic range of a species by finding the distribution that has the maximum entropy constrained by the environmental conditions at recorded occurrence locations (Phillips et al., 2017). Maxent predicts environmental suitability, with better conditions represented by higher values (Phillips et al., 2006). This method tends to predict the largest possible suitable area consistent with the data (Merow et al., 2013). While careful consideration of the limitations and biases in the data must be taken, Maxent performs well when compared to presence-absence models (Derville et al., 2018).

In order to build the Maxent species distribution models, we used the Maxent function available within the dismo version 1.1-4 package in R (Hijmans et al., 2017). Maxent model settings were defined through the ENMevaluate function of the ENMeval package (Muscarella et al., 2014), which provided species-specific settings to generate models, such as feature classes and standardized multiplier values. The model with the lowest value of the Akaike's Information Criterion corrected

for small samples sizes (*AICc*) reflects both model's goodness-of-fit and complexity (Muscarella et al., 2014). We used the block as data partitioning method, which splits the data into four bins based on lines of latitude and longitude to divide occurrence localities as equally as possible (Muscarella et al., 2014). For model validation, we adopted the values of the area under the receiver-operator (ROC) curve (*AUC*) as indicators of the predictive skill of the model (Phillips et al., 2006), where *AUC* closest to a value of 1 would be a perfect model and *AUC* = 0.5 would indicate that the model performed no better than random.

Twenty percent of the sightings for each species were randomly selected as test data sets to evaluate the fit of the model and its predictive power through the evaluate function in the dismo package. Maps were exported in raster format with continuous values and were interpreted from a percentage of environmental suitability ranging from unsuitable (0%) to highly suitable (100%). For visualization purposes of the potential distributions of these three species across the study area in a binary map of presence/absence, these were built based on the threshold of equal test sensitivity and specificity.

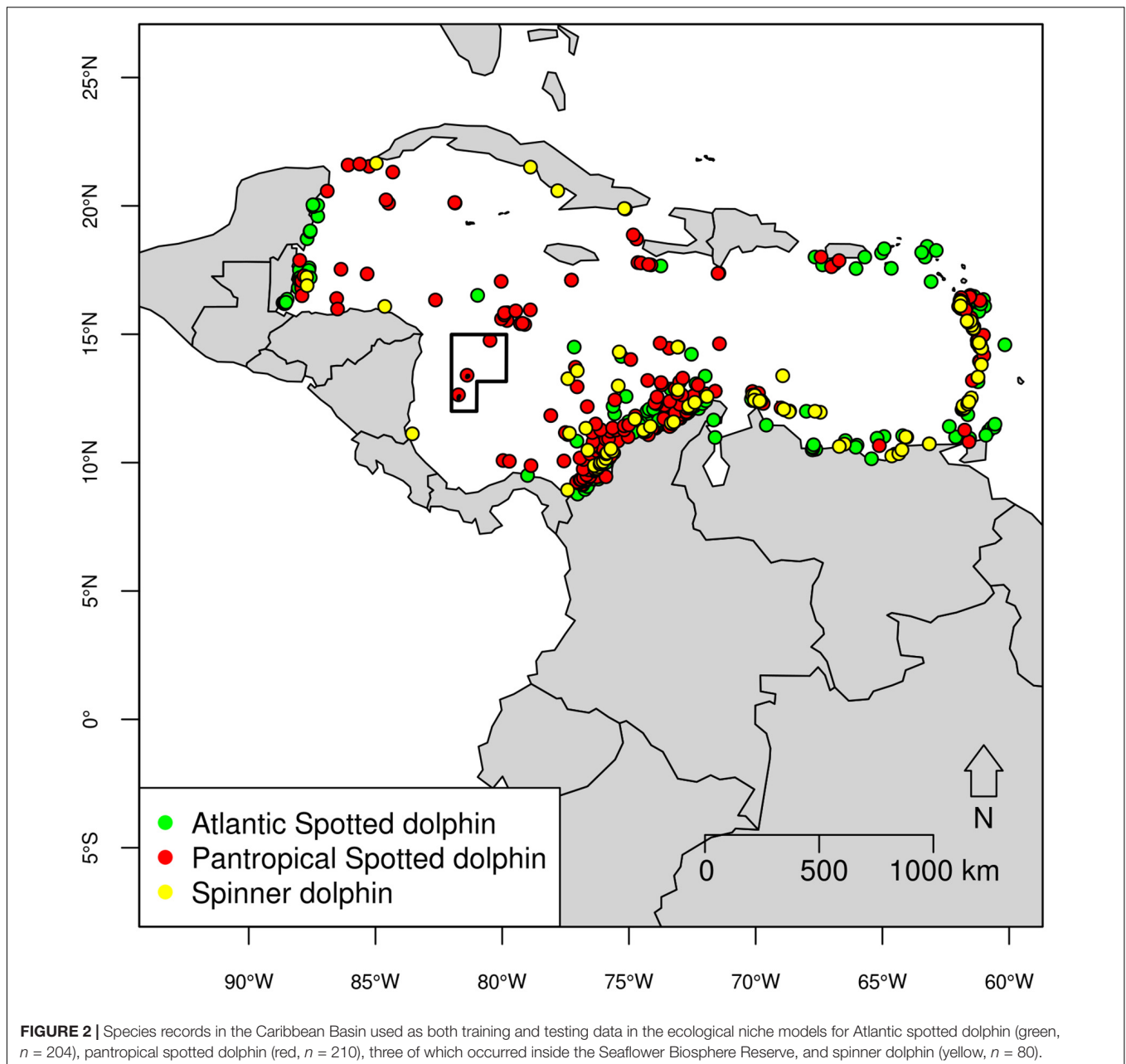## Statistical Comparisons of Distribution Patterns

We tested the null hypothesis that each species had similar distributions of the environmental variables using the non-parametric Kruskal–Wallis test followed by the Dunn test available in the dunn package (Dinno, 2017). The range and distributional properties of the environmental layers where species were recorded were represented as boxplots.

Comparative similarity measures among *Stenella* species and the niche identity test implemented in the dismo package were computed. Specifically, we estimated the "*D*" and "*I*" similarity statistics of Warren et al. (2008) using the functions niche overlap from predictions of species' distributions, where the resulting values ranges from 0 (no overlap) to 1 (the distributions are identical). We tested the null hypothesis that the ecological niche models of each species pair were identical using the function nicheEquivalency based on 499 randomizations. To visualize the degree of spatial overlap between the *Stenella* species distributions, we overlapped binary maps for the three pairwise combinations of species using the crop function in the raster package.

TABLE 2 | The ecological niche models with the best configuration for each species, the number of training and testing data, the *AUC* testing values and the relative contributions of the major environmental variables to the Maxent models with dynamic and static variables.

Species	Feature classes and regularization multipliers values	Training data	Testing data	*AUC* testing	Variable contribution (%)
Atlantic spotted dolphin	LQHP RM 3.5	163	41	0.852	Distance (30.49%) Mean Chl-a (22.88%) Bathymetry (22.68%)
Pantropical spotted dolphin	LQH RM 2.5	168	42	0.856	Distance (29.63%) Mean Chl-a (19.66%) Range SST (16.27%)
Spinner dolphin	H RM 2.5	64	16	0.854	Distance (57.94%) Mean Chl-a (26.84%) Slope (10.63%)

L, linear; Q, quadratic; H, hinge; P, product; RM, regularization multiplier.

FIGURE 2 | Species records in the Caribbean Basin used as both training and testing data in the ecological niche models for Atlantic spotted dolphin (green, *n* = 204), pantropical spotted dolphin (red, *n* = 210), three of which occurred inside the Seaflower Biosphere Reserve, and spinner dolphin (yellow, *n* = 80).
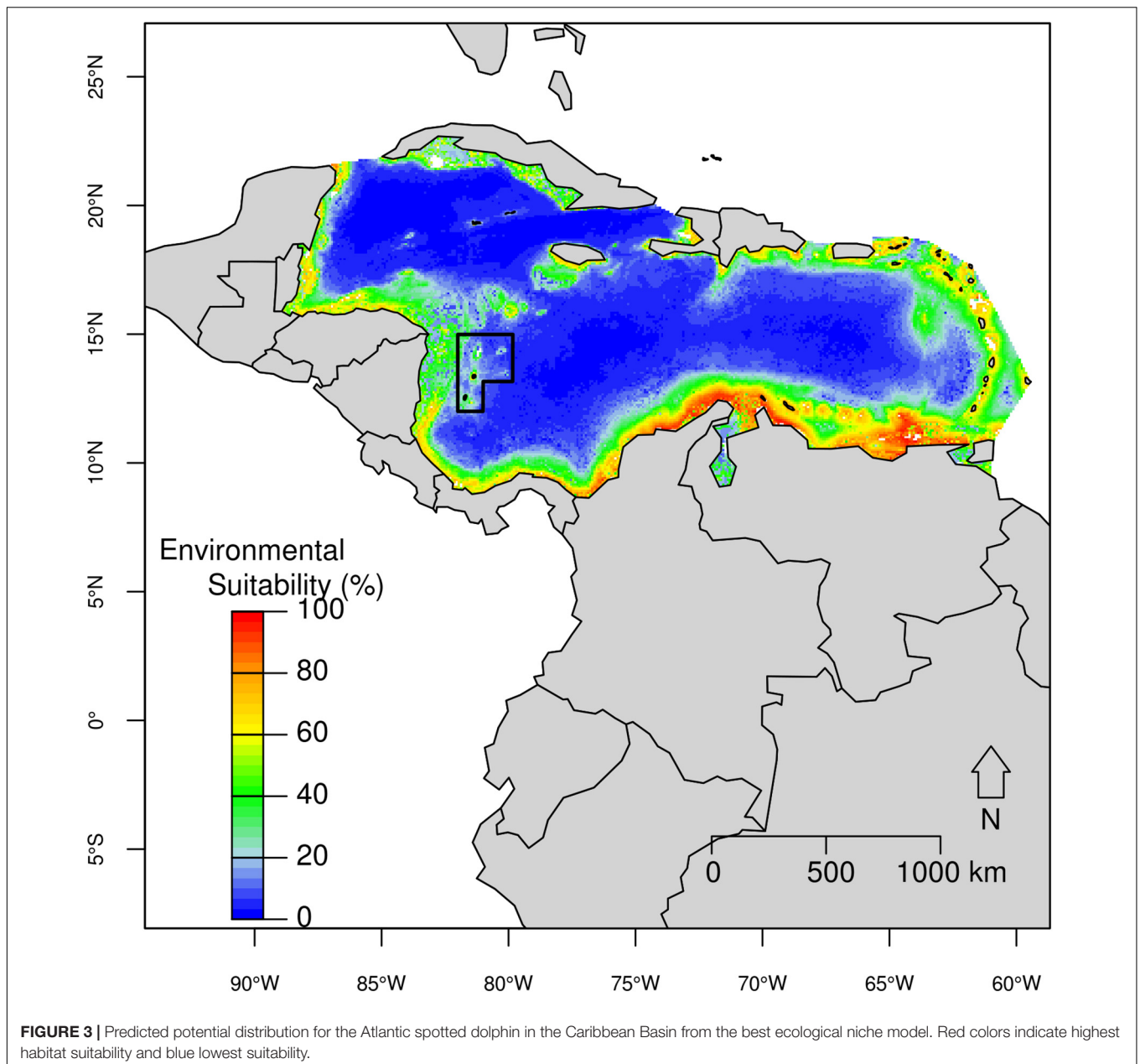
RESULTS

Ecological Niche Modeling

Ecological niche models were built based on seven uncorrelated environmental layers: bathymetry, distance to shore, slope, Mean SSS, Mean SST and Mean Chl-a, as well as Range SST. In total, 887 records of *Stenella* species were compiled (**Supplementary Table S1**), and after data cleaning 494 were kept (**Table 2** and **Figure 2**).

The model with the best configuration for each species is presented in **Table 2**. Ecological niche models incorporating dynamic and static variables returned *AUC* test values higher than 0.85 for all three species, indicating that these models had

a good performance. In general, distance to shore and Mean Chl-a were the environmental variables that contributed the most within all models (**Table 2**). The potential geographic range of distribution for each species, as predicted by the best models, is shown in **Figures 3–5**.

Atlantic Spotted Dolphin Ecological Niche Model

The predicted potential distribution map for the Atlantic spotted dolphin indicated that the areas closest to continental shorelines had the highest environmental suitability (>70%). Specifically a high suitability area was found mainly in the coastal region off mainland Colombia and more broadly, along the southeastern Caribbean, with oceanic areas and

FIGURE 3 | Predicted potential distribution for the Atlantic spotted dolphin in the Caribbean Basin from the best ecological niche model. Red colors indicate highest habitat suitability and blue lowest suitability.

particularly the SFBR presenting a low environmental suitability (**Figure 3**). High environmental suitability (higher than 80%) was observed in areas with bathymetry ranging from 9 m to 1,067 m (median = 77 m); distance to shore between 1 km and 12 km (median = 4 km); slope ranging from 1° to 113° (median = 24°); Mean SST between 25 and 27°C (median = 26.9°C); Range SST between 1.89 and 3.34°C (median = 2.55°C); Mean SSS ranging from 34.3 to 36.1 psu (median = 34.7 psu); and Mean Chl-a between 0.12 and 1.68 mg/m^3 (median = 0.64 mg/m^3).
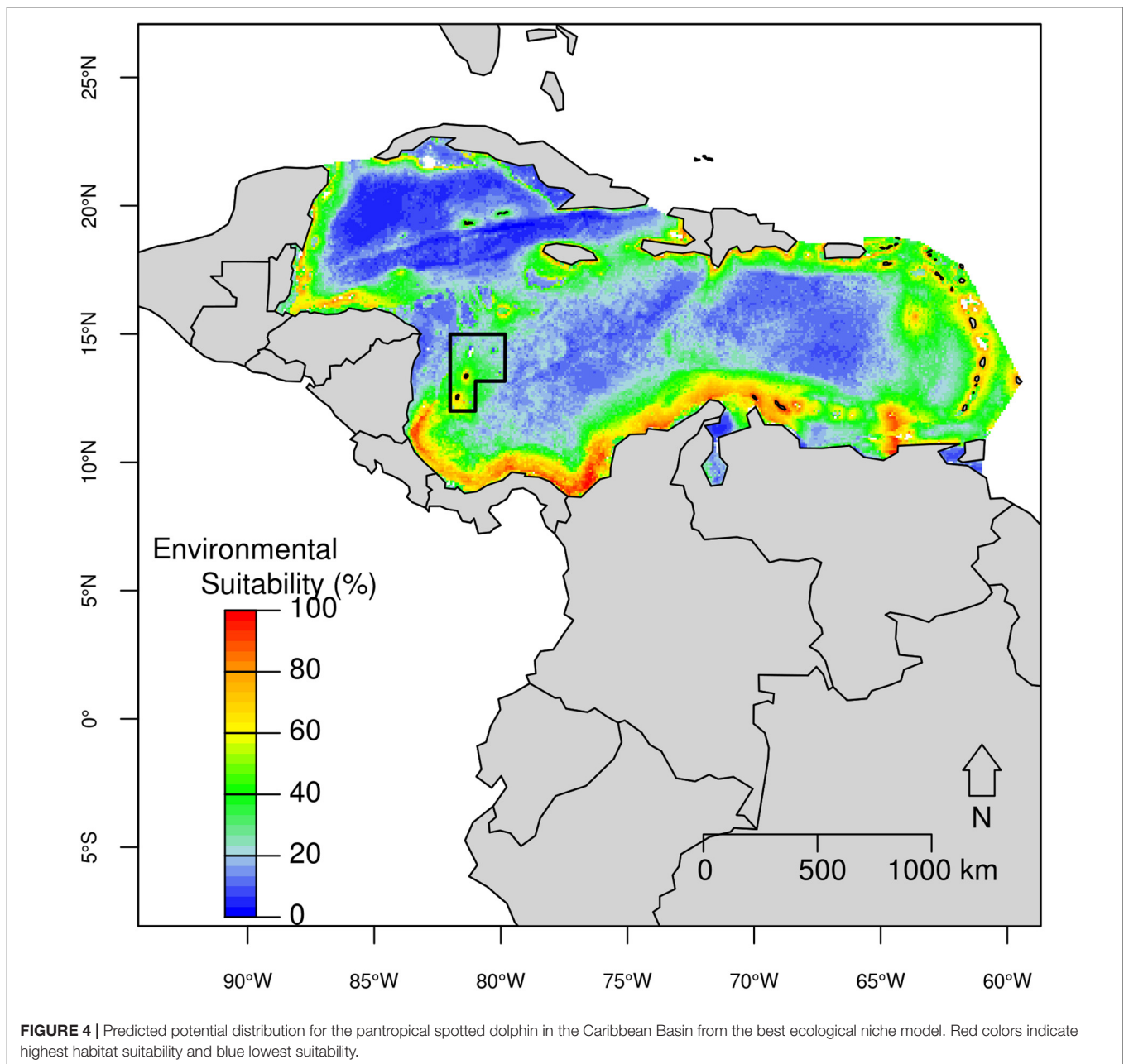
Pantropical Spotted Dolphin Ecological Niche Model

An environmental suitability higher than 60% was predicted for the pantropical spotted dolphin across most of the

Caribbean Basin, but mainly closer to the continent and nearby islands, including the SFBR (**Figure 4**). Records with suitability higher than 80% ranged in depth from 58 m to 2,215 m (median = 813 m); distance to shore between 3 km and 72 km (median = 42 km); slope ranging from 2° to 120° (median = 26°); Mean SST between 25.6 and 28.3°C; Range SST was between 1.1 and 4.1°C (median = 1.3°C); Mean SSS around 35 psu; and Mean Chl-a ranging from 0.12 to 1.12 mg/m^3 (median = 0.21). In the SFBR, environmental suitability around 60% was detected within the southern portion of the Reserve.

Spinner Dolphin Ecological Niche Model

The highest suitability (>70%) for spinner dolphins was predicted in waters surrounding islands or seamounts, and with
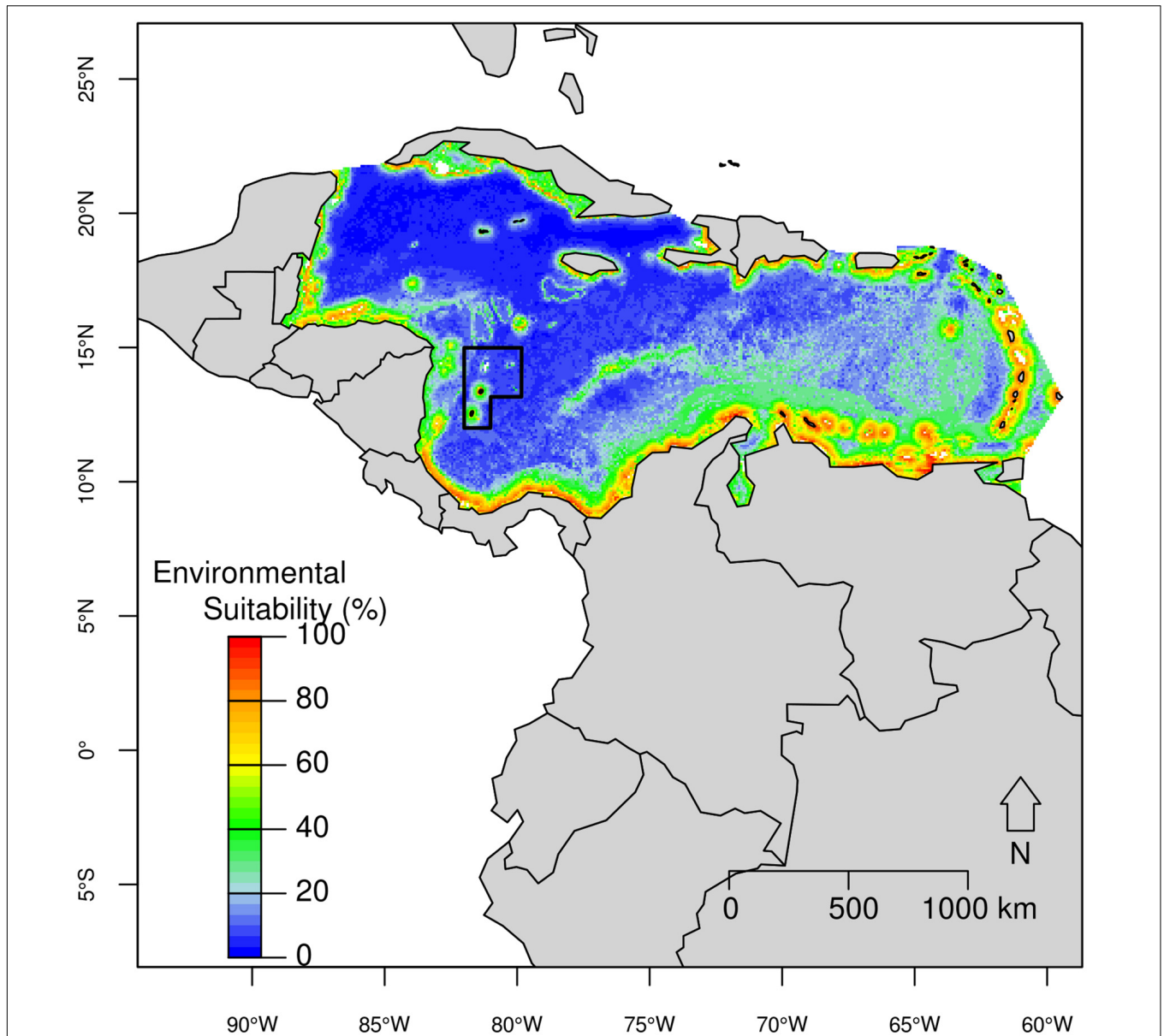
FIGURE 4 | Predicted potential distribution for the pantropical spotted dolphin in the Caribbean Basin from the best ecological niche model. Red colors indicate highest habitat suitability and blue lowest suitability.

a steeper slope (**Figure 5**), in almost all coastal areas in the Caribbean including surrounding islands. High environmental suitability (over 80%) corresponded to areas with bathymetry ranging from 30 m to 1,599 m (median = 620 m); distance to shore between 1 km and 9 km (median = 5 km); slope ranging from 1° to 165° (median = 106.5°); Mean SST between 25.4 and 27.7°C (median = 27.2°C); Range SST between 2.14 to 4°C (median = 2.5°C); Mean SSS ranging from 34.6 to 35.9 psu (median = 35.1 psu); and Mean Chl-a between 0.11 and 1.7 mg/m^3 (median = 0.38 mg/m^3). The SFBR exhibited a high habitat suitability for spinner dolphins, primarily around the insular region, where environmental suitability reached 72% (e.g., around San Andrés Island).

Niche Overlap and Identity Test

Pairwise overlap for the three *Stenella* species is presented in **Table 3**. We found high "*I*" and "*D*" similarity statistic scores for all pairwise comparisons, indicating that ecological niches were broadly similar among Atlantic spotted dolphins, pantropical spotted dolphins, and spinner dolphins in the Caribbean Basin. Niche identity tests did not reject the null hypotheses that assumed the niches were identical between pairwise *Stenella* species comparisons (**Table 3**).

However, our results indicated that while the distribution of Atlantic spotted dolphins and spinner dolphins showed the highest statistical similarity, Atlantic and pantropical spotted dolphins shared the lowest similarity values. In general, all three

FIGURE 5 | Predicted potential distribution for the spinner dolphin in the Caribbean Basin from the best ecological niche model. Red colors indicate highest habitat suitability and blue lowest suitability.

TABLE 3 | Metrics obtained in niche overlap comparison and niche identity tests conducted pairwise between *Stenella* species.

	Niche overlap		Niche identity	
Pairwise combinations	**D similarity statistics**	**I similarity statistics**	**D similarity statistics**	**I similarity statistics**
Atlantic spotted dolphin *versus* pantropical spotted dolphin	0.73	0.94	0.71 (*p*-value = 1)	0.92 (*p*-value = 1)
Atlantic spotted dolphin *versus* spinner dolphin	0.80	0.96	0.76 (*p*-value = 0.99)	0.95 (*p*-value = 0.98)
Pantropical spotted dolphin *versus* spinner dolphin	0.78	0.96	0.67 (*p*-value = 0.99)	0.90 (*p*-value = 1)

species coincided in some areas, according to the overlap map based on the threshold of equal test sensitivity and specificity (**Table 4** and **Figures 6–8**). All species overlapped in their distributions in coastal areas of the southern and southeastern Caribbean off Colombia, Venezuela, and surrounding areas in the Antilles, as well as in the SFBR. Nonetheless, while

TABLE 4 | Threshold of equal test sensitivity and specificity obtained for each model generated among three *Stenella* species in the Caribbean Basin.
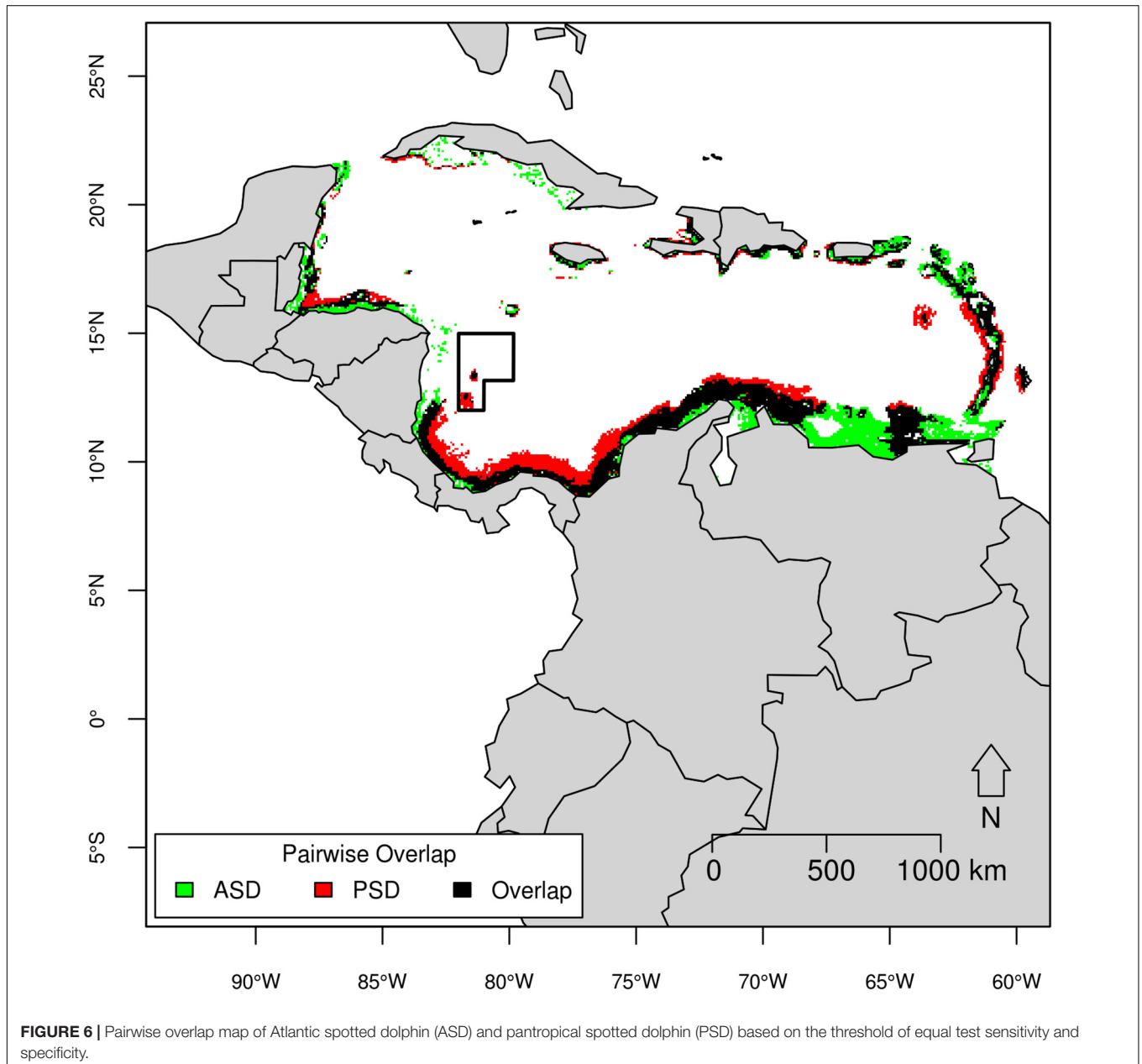
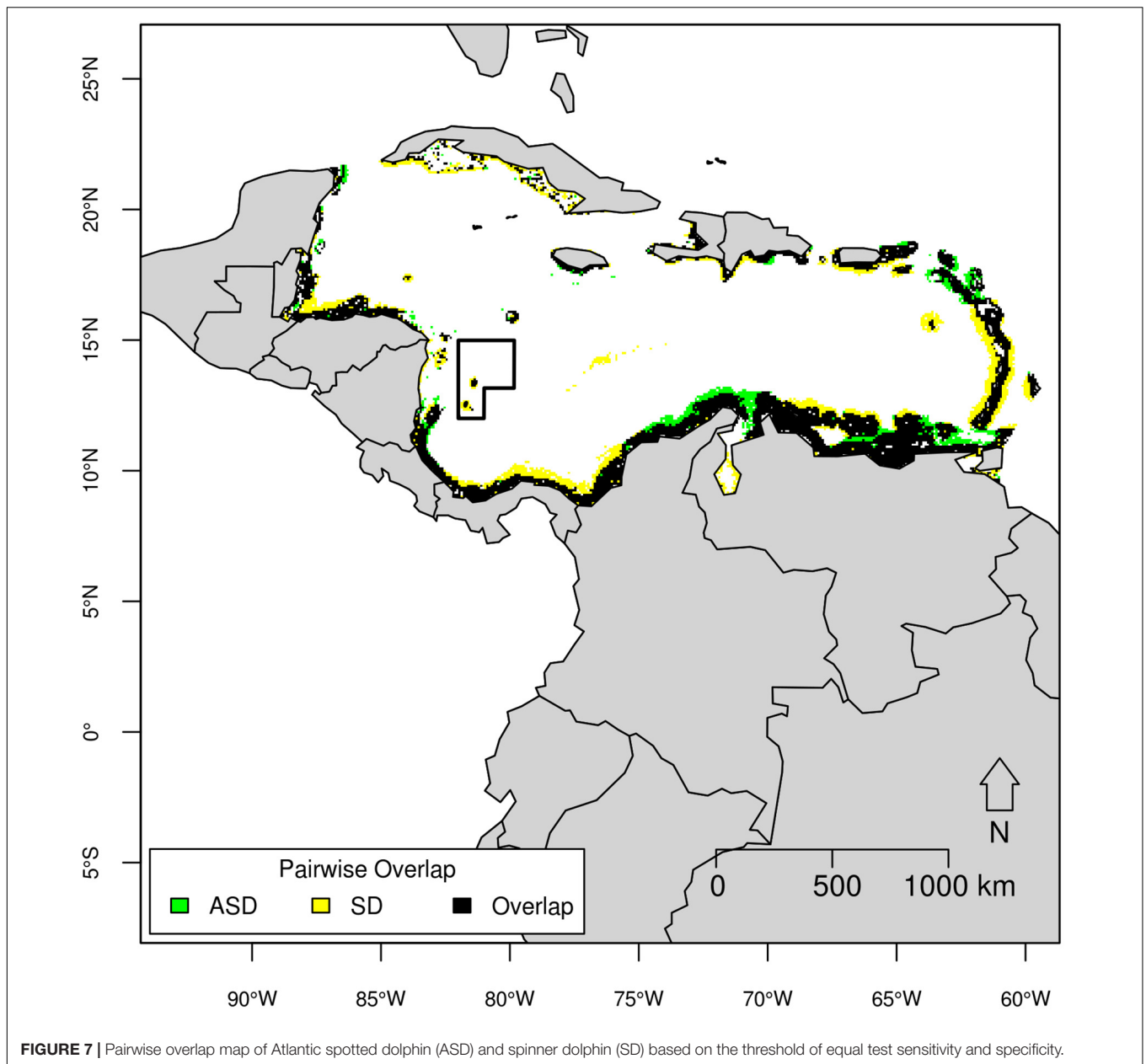| Species	Threshold of equal test sensitivity and specificity
Atlantic spotted dolphin	0.432
Pantropical spotted dolphin	0.516
Spinner dolphin	0.365

the distribution of pantropical spotted dolphins included more oceanic waters around 1,000 m deep, spinner dolphins appeared to occupy areas closer to island chains, and Atlantic spotted dolphins appeared to be more restricted to coastal/neritic waters.

Statistical Comparisons of Environmental Variables

The median values of the environmental variables for each species indicated significant interspecific differences (**Table 5** and **Figure 9**). The null hypothesis of equal medians for bathymetry, distance to shore, slope, Mean Chl-a, Mean SST and Range SST was rejected (Kruskal–Wallis test, $p < 0.05$).

Pantropical spotted dolphins had the highest median bathymetry, distance to shore, Mean SST, and the lowest median Mean Chl-a. In other words, pantropical spotted dolphins occupied areas of low phytoplankton biomass, and deeper (up to about 1,000 m) and warmer waters. Atlantic spotted dolphins and pantropical spotted dolphins differed in relation to bathymetry,

FIGURE 6 | Pairwise overlap map of Atlantic spotted dolphin (ASD) and pantropical spotted dolphin (PSD) based on the threshold of equal test sensitivity and specificity.

FIGURE 7 | Pairwise overlap map of Atlantic spotted dolphin (ASD) and spinner dolphin (SD) based on the threshold of equal test sensitivity and specificity.
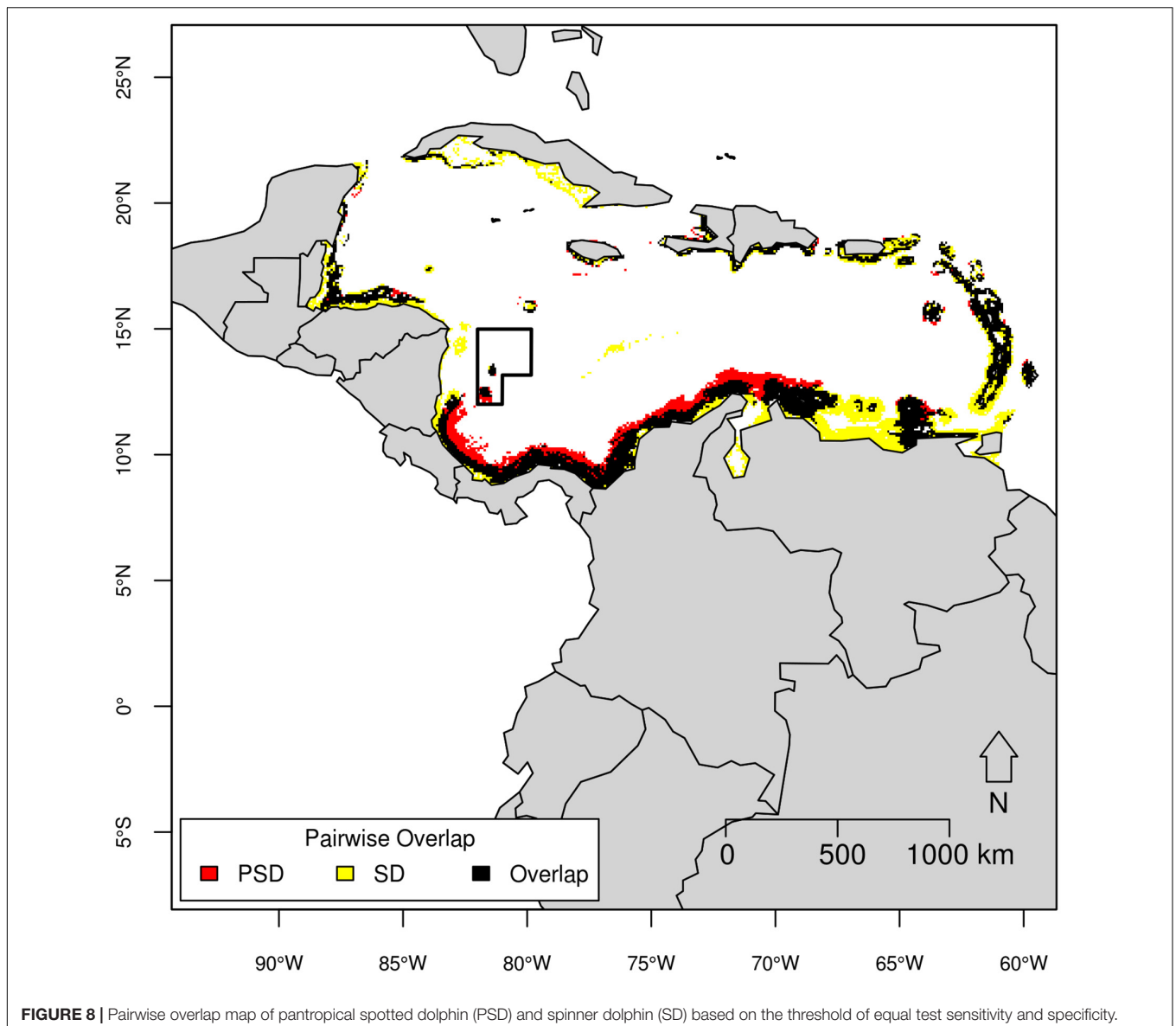
slope, distance to shore, Range SST and Mean Chl-a, with the former occurring in shallow waters closer to the shore, with lower slope values and Mean SST but higher productivity. Likewise, spinner dolphins occurred in areas surrounding the coast, with more phytoplankton biomass, and in shallower waters, although in regions characterized by a steeper slope.

DISCUSSION

This study established a series of potential "baseline" ecological niche models for Atlantic spotted dolphins, pantropical spotted dolphins and spinner dolphins. These models were used for assessing their distribution patterns in the Caribbean Basin,

particularly in the SFBR. In this study, we provide the first characterization of the environmental niches of three *Stenella* species and their potential distributional patterns in the Caribbean Basin. Our findings show that distance to coastline and Mean Chl-a play an important role that influences the potential distribution of these three species in the region.

Species of *Stenella* are widely distributed in the Caribbean Basin, yet their patterns have been poorly studied. Small delphinids of the genus *Stenella* carry out long-range movements of up to 2,500 km (Reilly, 1990), presumably associated with prey availability dynamics (Davis et al., 2002). In fact, ecological niches for dolphins appear to be defined by variables that affect distribution and abundance of resources they rely upon (Baumgartner et al., 2001; MacLeod et al., 2008).

FIGURE 8 | Pairwise overlap map of pantropical spotted dolphin (PSD) and spinner dolphin (SD) based on the threshold of equal test sensitivity and specificity.

The availability of dolphin prey depends mainly on primary productivity, which is highly variable in the oligotrophic waters of the Caribbean Basin (Corredor, 1979; Müller-Karger and
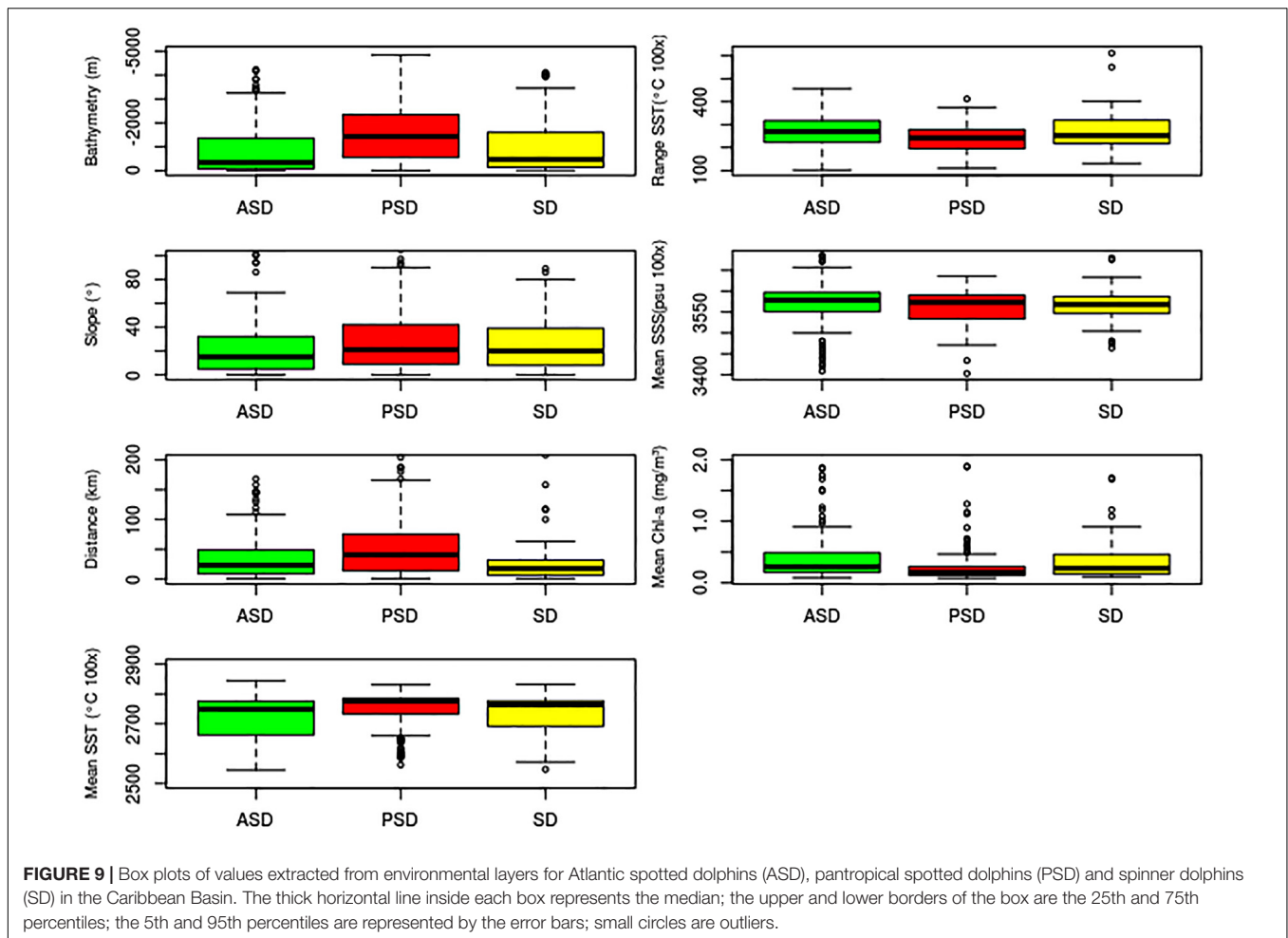
TABLE 5 | Results of the Kruskal–Wallis test for comparing environmental variables between Atlantic spotted dolphins, pantropical spotted dolphins and spinner dolphins.

Environmental variable	Kruskal–Wallis (X^2)	p-value
Bathymetry	40.567	1.552e-09
Distance to shore	18.999	7.487e-05
Bathymetric slope	8.1875	0.01668
Mean annual sea surface temperature	17.65	0.000147
Annual range in sea surface temperature	14.7705	0.0006203
Mean annual sea surface salinity	4.84	0.08892
Mean annual chlorophyll-a concentration	35.297	2.165e-08

Aparicio, 1994; Aguirre, 2014). In the first part of the year, primary productivity concentrates along the continental coasts of Colombia and Venezuela, while shifting to Caribbean islands such as Puerto Rico, the Virgin Islands and the Antilles in the second part (Müller-Karger et al., 1989; Müller-Karger and Aparicio, 1994). This variability enables *Stenella* species, such as pantropical spotted dolphins and spinner dolphins, to exploit oceanic and deeper-water environments given their long-distance movement capabilities.

Coastal-marine ecosystems such as coral reefs and seagrass beds host a high biodiversity and productivity that provide food resources for local and oceanic biological communities. The SFBR appears to be an important area for dolphins in the Caribbean Basin not only because it contains the largest open-ocean coral reefs in the Caribbean, but because it also holds extensive and healthy seagrass beds (Taylor et al., 2013). Consequently, the overlap in the ecological niche of pantropical spotted dolphins

FIGURE 9 | Box plots of values extracted from environmental layers for Atlantic spotted dolphins (ASD), pantropical spotted dolphins (PSD) and spinner dolphins (SD) in the Caribbean Basin. The thick horizontal line inside each box represents the median; the upper and lower borders of the box are the 25th and 75th percentiles; the 5th and 95th percentiles are represented by the error bars; small circles are outliers.

and spinner dolphins in the area is not surprising. In contrast, Atlantic spotted dolphins primarily inhabit coastal environments throughout most of their range, a distribution pattern similar to the one previously described in the Western South Atlantic Ocean by do Amaral et al. (2015). Productive coral reefs and seagrass beds are also found along the Colombian mainland coast, notably in Morrosquillo Gulf, the Rosario and San Bernardo Archipelago, Santa Marta, and the Tayrona region (Garzón-Ferreira et al., 2001).

Water temperature has been shown to be an important attribute of cetaceans' ecological niches (MacLeod, 2009). In the Caribbean Basin, the southern region along the coast of Colombia and Venezuela exhibits low SST associated with coastal upwelling, mainly off La Guajira region (Colombia) in the central Caribbean and around Margarita Island (Venezuela) in the eastern Caribbean (Gordon, 1967; Müller-Karger et al., 1989; Andrade et al., 2003; Andrade and Barton, 2005; Lonin et al., 2010; Paramo et al., 2011). This upwelling generates a high primary productivity (Corredor, 1979; Andrade et al., 2003; Andrade and Barton, 2005; Criales-Hernández et al., 2006; Arévalo-Martínez and Franco-Herrera, 2008; Lonin et al., 2010) that has been related to the occurrence of other dolphin species in the area (Farías-Curtidor et al., 2017). Considering that low

SST was an important descriptor of habitat suitability for Atlantic spotted dolphins, it is not surprising that they were preferentially found in Caribbean environments defined by shallow waters with lower temperatures and elevated primary productivity.

Bathymetry is another important predictor of Atlantic spotted dolphin habitats in the Caribbean Basin. Similar to what has been reported for the Gulf of México and the Western South Atlantic Ocean, this species showed a preference for shallower waters along the Colombian Caribbean (Davis et al., 1998; do Amaral et al., 2015). Atlantic spotted dolphins feed preferentially on coastal prey (Perrin et al., 1994), so their presence in shallow waters is frequent (Davis et al., 1998, 2002). These coastal habits could suggest that this species is not very cosmopolitan in the Atlantic Ocean, showing restricted movements across northern and southern portions of this ocean. Genetic studies have shown that individuals from the Colombian Caribbean are closely related to those population units from locations as far as west and east north Atlantic (Mesa-Gutiérrez et al., 2015); while populations from Azores and Madeira, which show high connectivity between them (Quérouil et al., 2010), resulted closely related to those from the Western North Atlantic and Brazil (Caballero et al., 2013; Mesa-Gutiérrez et al., 2015). Additionally, Atlantic spotted dolphins along the Brazilian coast

also show genetic (Caballero et al., 2013) and morphological divergence (Moreno et al., 2005) associated with differences in environmental conditions between southern and northern Brazilian populations (do Amaral et al., 2015). Furthermore, Atlantic spotted dolphin populations along the east coast of the United States and Gulf of Mexico show significant population structure due mainly to an extensive continental shelf that promotes differential habitat structuring and hence, the aggregation of resources in specific zones to be exploited (Adams and Rosel, 2006). All these evidences suggest that environmental conditions associated with coastal habitats could drive differentiation between Atlantic spotted dolphins across the Atlantic Ocean although more studies are needed to support this assumption.

Similar to Atlantic spotted dolphins, spinner dolphins occur in productive regions surrounding coastlines but with steeper slopes, mainly near islands (**Figure 7**). Indeed, the niche for these two species overlapped in much of coastal areas around the Caribbean Basin, except in waters surrounding islands such as in the SFBR, which is characterized by a pronounced slope (mean = 4.5°). The slope had a considerable contribution for the spinner dolphin model, preferred by this species due to the vertical and horizontal migration of mesopelagic fish considered an important part of their diet (Benoit-Bird and Au, 2003; Thorne et al., 2012).

Pantropical spotted dolphins also appeared to prefer waters around islands, but are present in deeper waters, as reported in the Gulf of Mexico (Davis et al., 1998) and in the Western South Atlantic (do Amaral et al., 2015). SST had a considerable contribution to the species' model, indicating that offshore pantropical spotted dolphins are usually found in warm tropical waters, as reported previously in the Western South Atlantic (do Amaral et al., 2015).

Although the *Stenella* species analyzed here showed differences in their environmental requirements in the Caribbean Basin, in general both spotted and spinner dolphins occupied similar habitats in the region. It has been suggested that Atlantic spotted dolphins and pantropical spotted dolphins are sympatric in the Atlantic Ocean (Perrin and Hohn, 1994). Likewise, associations between pantropical spotted dolphins and spinner dolphins have been documented in the Atlantic (Silva et al., 2005). However, do Amaral et al. (2015) suggested that *Stenella* dolphins, particularly the three species considered for the current study, could exhibit niche partitioning and spatial segregation in the Western South Atlantic. Davis et al. (1998) also reported differences in distribution of these three *Stenella* species along the Gulf of Mexico. These differences have been related not only to oceanographic conditions (do Amaral et al., 2015), but also to prey distribution and feeding preferences among *Stenella* species (Davis et al., 2002). However, in areas where nutrients are scarce, feeding preferences facilitate that small cetaceans share their habitat (Davis et al., 2002). In the Caribbean Basin, Atlantic spotted, pantropical and spinner dolphins seem to overlap much more in their distributions, particularly in high-productivity areas.

These findings generate special concern regarding climate change due to the effects on marine and coastal productive ecosystems such as coral reefs. Particularly, these ecosystems have been heavily affected in the Caribbean Basin (Connell, 1997; Pandolfi et al., 2003), allowing the increase in macroalgae coverage (Mumby et al., 2007) and the consequent decreases in local biodiversity. Similarly, prey distribution could be affected due to increases in water temperature (Learmonth et al., 2006; MacLeod, 2009). These shifts in prey availability can affect distributional patterns on dolphins in the Caribbean Basin (Learmonth et al., 2006; MacLeod, 2009; Ramos et al., 2016), which could force them to spend more time traveling in oceanic waters looking for resources.

While oceanic areas in the Caribbean Basin appear to be potentially important for *Stenella* dolphins, most studies have taken place in coastal waters. Therefore, the distribution patterns suggested in this study, based only on sightings, do not predict suitable habitat beyond the known records of *Stenella* in the Caribbean Basin. Although efforts have increased in the region to advance marine mammal research, there is still a large knowledge gap to improve the management of such species. Areas of very low coverage (like the center of Western Caribbean where no research has been done) could contribute to the habitat close to shore and of specific depths being deemed highly suitable. This is the case for the SFBR, which is an oceanic area poorly studied with regarding marine mammals. This Reserve holds high local biodiversity related to coastal marine ecosystems that are potentially important for dolphins' distribution as foraging hotspots. The SFBR appears to be more suitable in its southern portion for pantropical and spinner dolphins, mainly around the islands, but their ecological and oceanographic conditions could allow the occurrence of other small cetacean species. Future research should focus on this protected area, to assess if it should be considered as a priority area for cetacean species in the Caribbean Basin.

AUTHOR CONTRIBUTIONS

DB-B, PC-C, NF-C, RL-N, PB, JB-J, LB, DC-M, JL, JM, RM-G, BdM, ER, VR, and DP contributed to the acquisition of field data. DB-B, KBA, and NF-C organized the data and compiled the literature. DB-B and KBA conceived and designed the experiments, analyzed the data, and wrote the manuscript. KBA performed the experiments. DB-B, KBA, PC-C, NB-A, IM, JB-J, DC-M, JL, RM-G, BdM, ER, and DP contributed to the manuscript writing. All authors have approved the final version of the manuscript.

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SUPPLEMENTARY MATERIAL

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