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Potential distribution of Guiana dolphin (*Sotalia guianensis*): a coastal-estuarine and tropical habitat specialist

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Ecological niche models (ENMs) predict where species can occur in accordance with environmental factors. Suitability maps are generated through models to identify habitats more or less adapted to the species. Published works on the distribution and habitat use of Guiana dolphin, *Sotalia guianensis*, are limited to fine spatial scales. Here, we aimed to predict the potential geographical distribution of Guiana dolphins through ENMs and generate a map of suitable habitats for the species. Data were collected between 1997 and 2015 in Brazil, French Guiana, and Colombia. The environmental data were obtained from MARSPEC database with a cell resolution of 10 × 10 km. For modeling, 99 of the 859 initial occurrence points of the species were considered after rarefaction. Seven environmental variables were selected through factorial analysis: bathymetry, distance to shore, bathymetric slope, sea surface salinity (minimum monthly and annual range), and sea surface temperature (mean annual and annual range). Results from five distinct algorithms were assembled to generate the distribution model. Our findings show potential areas in shallow platforms of the continental margin of South and Central America, including regions where the species has never been reported, such as the Pacific Ocean, the Gulf of California, the Gulf of Mexico, and the oceanic islands in the Caribbean Sea. The absence of Guiana dolphins in these regions may be due to geographical (linking of North and South America), physical (water temperature), and biological (competition, limited ability to dispersal) limiting factors. The models suggest that the presence of other species of coastal dolphin may be an important limiting factor for the Guiana dolphin at both extremes of its distribution. The Guiana dolphin is habitat specialist with a clinal potential geographic distribution concentrated in tropical and subtropical shallow and coastal waters of the continental shelf of the western Atlantic Ocean. This more restricted distribution than reported by IUCN and other studies suggests a cautionary approach to its conservation status due to limited dispersal abilities and high overlap with human activities.

Key words: Cetartiodactyla, Delphinidae, ecological niche models, *Sotalia*, suitability maps

Os modelos de nicho ecológico (ecological niche models - ENMs) promovem o conhecimento das interações de organismos com o ambiente, fornecendo previsões de onde as espécies podem ocorrer de acordo com fatores ambientais. A partir dessas previsões, é possível identificar habitats mais ou menos adequados para a ocorrência das espécies, de acordo com os mapas de distribuição potencial gerados. O boto-cinza, *Sotalia guianensis*, é uma espécie costeira muito estudada, porém as publicações sobre sua distribuição e uso do habitat se limitam a escalas espaciais locais. O presente estudo teve como objetivo modelar a distribuição geográfica potencial do boto-cinza, baseando-se em técnicas de ENMs e gerar um mapa de distribuição geográfica potencial da espécie. As coordenadas geográficas de presença da espécie foram coletadas em expedições embarcadas entre 1997 e 2015 no Brasil, Guiana Francesa e Colômbia, através de parcerias com instituições e pesquisadores. As variáveis ambientais foram obtidas a partir do banco de dados MARSPEC com resolução de 10 km. Para modelagem, 99 dos 859 pontos de ocorrência inicial da espécie foram considerados após rarefação. Sete variáveis ambientais foram determinadas através da análise fatorial: batimetria, distância da costa, declividade, salinidade (mínima mensal e taxa de variação anual) e temperatura da superfície do mar (média anual e taxa de variação anual). Os resultados de cinco algoritmos distintos foram reunidos para gerar o modelo de distribuição. Os ENMs gerados nesse trabalho apontaram áreas potenciais para a distribuição do boto-cinza em plataformas rasas da margem continental da América do Sul e Central. Os modelos também apontaram como áreas potenciais diversas regiões onde não há registros de ocorrência da espécie, como por exemplo, áreas no Oceano Pacífico, Golfo da Califórnia, Golfo do México e ilhas do Mar do Caribe. Sugerimos que a ausência do boto-cinza nessas regiões pode estar relacionada a aspectos geográficos (e.g., união entre os hemisférios), físicos (e.g., temperatura da água) e biológicos (e.g., competição, baixa capacidade de dispersão). Os modelos também sugerem que a presença de outras espécies de golfinhos costeiros pode ser um importante fator limitante para o boto-cinza em ambos os extremos de sua distribuição. O boto-cinza é um especialista de habitat com uma distribuição geográfica potencial clinal concentrada em águas tropicais e subtropicais rasas e costeiras da plataforma continental do oeste do Oceano Atlântico. Esta distribuição, mais restrita do que a relatada pela IUCN e outros estudos, sugere uma abordagem cautelosa de seu estado de conservação devido à limitada capacidade de dispersão e alta sobreposição com as atividades humanas.

Key words: Cetartiodactyla, Delphinidae, mapas de adequabilidade, modelos de nicho ecológico, *Sotalia*

Knowing the potential distribution of a species makes possible an assessment of its extinction risk. Mathematical and computational analyses developed in the last decades assist in understanding the geographical distribution of species based on the concept of the ecological niche (Peterson 2003; Jiménez 2005; Peterson et al. 2011; Silva et al. 2014; Caruso et al. 2015). The ecological niche of a species was defined by Hutchinson (1957) as an *n*-dimensional hypervolume, where "*n*" is the number of environmental factors that compose the species niche. These factors influence the distribution of species at different spatial scales. Environmental condition constrains species' distributions as a result of broad-scale processes. In addition, the interactions between species and their effects on the land or seascape can constrain the distribution of species at a finer scale (Pearson and Dawson 2003; Soberón and Nakamura 2009; Peterson et al. 2011).

The ecological niche of cetaceans primarily is defined by water temperature, depth, and other factors defining the distribution and abundance of their prey (MacLeod 2009). However, the habitat of coastal dolphins also is determined by various environmental and anthropogenic factors that vary among areas according to characteristics of geography, meteorology, and human activities. Among the environmental factors that influence the distribution of coastal dolphins are: distance to coast and to river mouth (Parra et al. 2006; Rossi-Santos et al. 2006; Herra-Miranda et al. 2015); proximity to reefs and islands (Melly et al. 2018); distance to seafood farms and fishing ground seabed slope and depth (Torres et al. 2003; Azevedo et al. 2007; Gross et al. 2009; Booth et al. 2013); swell characteristics (Dittmann et al. 2016); and tidal phase (Li et al. 2018). Among the anthropogenic factors are: fishing ground; habitat degradation due to the development of human activities such as agriculture, aquaculture, and urban development (Karczmarski et al. 2017; Tardin et al. 2020); as well as related activities such as pile-driving (Leunissen et al. 2019) and boat traffic (Allen and Read 2000).

Dolphins with coastal habits are impacted by human activities and disturbance to nearshore environments that ultimately may make some species vulnerable to extinction at a global level. For example, according to IUCN Red List of threatened species, Franciscana (*Pontoporia blainvillei*) is vulnerable to extinction (Zerbini et al. 2017), Vaquita (*Phocoena sinus*) is critically endangered (Rojas-Bracho and Taylor 2017), and Baiji (*Lipotes vexillifer*) possibly is extinct (Smith et al. 2017). The Guiana dolphin, *Sotalia guianensis* (Van Beneden 1864) is considered "near threatened" by IUCN at a global level, despite uncertainties regarding its abundance, population dynamics, and mortality rates (Secchi et al. 2018). In Brazil, the Guiana dolphin has been considered "vulnerable" since 2014 in the official national list of endangered species of fauna (Brasil 2014) because the population decline is expected to be over 30% in three generations due to the increasing anthropogenic pressure suffered by the species.

The Guiana dolphin often is found in shallow waters and coastal regions (Borobia et al. 1991; Da Silva et al. 2010), but also occurs up to 70 km from the coast, on the Abrolhos Bank where depths are mostly less than 40 m (Borobia et al. 1991; Rossi-Santos et al. 2006). The species is endemic to the Atlantic coast of Central and South America, from southern Brazil (27°35′S, 48°35′W—Simões-Lopes 1988) to Nicaragua (14°53′N, 83°22′W—Edwards and Schnell 2001). Despite the Guiana dolphin being a well-studied species, there are gaps in knowledge of its ecology, such as its potential distribution. Most studies on spatial and habitat use are restricted to the local scale, i.e., to Guiana dolphins that frequent a single bay or estuary and nearby coastal waters (e.g., Azevedo et al. 2007; Dias et al. 2009; Godoy et al. 2015). Thus, studies focusing on habitat relationships on a broad spatial scale could shed light on ecological relationships of the species. A detailed mapping of its distribution is one of the research actions listed by Rosas et al. (2018) that are needed to ensure conservation of the species.

Ecological niche models (ENMs) promote knowledge of animal interactions with the environment, providing predictions as to where the species may occur on the basis of environmental factors. Based on these predictions, it is possible to identify habitats that are suitable to the occurrence of the species, in accordance with the generated potential distribution maps (Peterson et al. 2011).

Here, we aimed to model the potential geographic distribution of the Guiana dolphin, using ENMs, generating an environmental suitability map for the species and discussing the potential factors that mold its distribution.

Materials and Methods

Ecological niche models were generated for the Neotropical region (−119°W to −23°W and −60°S to 28°N), using ArcGIS 10 and the R computing environment (R Development Core Team 2018). ENM techniques are structured on three principal components: i) a set of species occurrences; ii) environmental variables; and iii) a mathematical algorithm hypothesized to predict potential distributions of species (Franklin 2010; Peterson et al. 2011).

Occurrence data.—The occurrence information are records of where the Guiana dolphin have been observed between 1997 and 2015 from vessel and aerial surveys by different institutions and researchers (Table 1). The records were compiled and plotted with ArcGIS software to exclude erroneous records (i.e., locations on land, offshore, and outside the surveyed area). To reduce spatial autocorrelation between the records and minimize biases in modeling, we applied the spatially rarefy occurrence data tool of SDMtoolbox in ArcGIS. This tool reduces occurrence localities to a single point within a specified distance (Brown 2014), which in this case was 10 km Euclidean distance.

In an attempt to illustrate the representativeness of the points used in the modeling, we selected all the articles in the Web of Science database on Guiana dolphins that included visual or acoustic monitoring of wild populations (n = 116), excluding studies based on stranded or captive animals. We counted the number of published studies (n = 139) for each monitoring area and georeferenced them.

Environmental data.—Environmental data were obtained from the MARSPEC database (www.marspec.org) at a cell resolution of 5 arcminutes (9.25 km at the equator) in raster format. MARSPEC is a set of high-resolution GIS database of ocean climate and geophysical data layers for all the oceans in the world (Sbrocco and Barber 2013). The geophysical variables of MARSPEC were derived from the SRTM30_PLUS high-resolution bathymetry data set (Becker et al. 2009). The bioclimatic variables of MARSPEC were derived from NOAA's World Ocean Atlas and NASA's MODIS satellite imagery (Sbrocco and Barber 2013).

Eleven environmental variables resulting in layers were generated for this study: bathymetry, distance to shore, bathymetric slope, sea surface salinity—SSS (mean annual, minimum monthly, maximum monthly, annual range, and annual variance), and sea surface temperature—SST (mean annual, annual range, and annual variance). To avoid the use of correlated variables and reduce bias in the analyses, we used the "psych" package for factorial analysis and select the most informative environmental variables. When two variables were correlated, their relevance in the biology of the species was a criterion of choice or higher factor loadings. For example, of the three variables derived from salinity (minimum, mean, and maximum) that stood out in the first factor (see results, Table 2), the minimum salinity was chosen because the species is not found in freshwater environments hence minimum salinity is a possible limiting factor for its occurrence.

Algorithms.—Ecological niche models are calculated from different algorithms because there is no single algorithm that is ideal and appropriate for all the objectives of studies on spatial distribution (Marmion et al. 2009; Li and Wang 2013). We used five algorithms: Bioclim, Gower, Mahalanobis, Support Vector Machines (SVM), and Maximum Entropy (MaxEnt) (Lima-Ribeiro and Diniz-Filho 2013). Bioclim is the simplest model and is based on bioclimatic envelopes, whereby all the areas presenting values within the intervals tolerated by the species in relation to the studied variables are selected (in the format of a rectilinear envelope—Busby 1986, 1991). These areas indicate the potential distribution for a species. This algorithm does not demonstrate a continuous gradient in habitat suitability but indicates if an area is suitable or not for the survival of the species in accordance with its bioclimatic envelope (Busby 1991).

Gower (models based on environmental distances—Carpenter et al. 1993) and Mahalanobis distance (models based on multivariate analyses) algorithms (Farber and Kadmon 2003) differ only in their method of calculating the models. In Mahalanobis distance, the "optimal" climatic conditions for the species are estimated from a multidimensional climatic space (Farber and Kadmon 2003). However, both algorithms assume the existence of an optimal environmental condition for the survival of the species, determined by a centroid of the environmental conditions in relation to

Table 1.—Data used for modeling the potential geographic distribution of *Sotalia guianensis* (1997–2015).

Year	Country/state	Records	Research
1997–2014	Brasil/PB, PE, SE, BA, ES	IBJ	Vessel survey
2002 and 2003	Brazil/BA	Maria do Socorro Santos Reis (Projeto MAMA)	Vessel survey
2008	Brazil/RN	Alexandre Douglas Paro	Vessel survey
2009–2011	Brazil/CE	Ana Carolina Meirelles	Vessel survey
2010	Brazil/BA	Meline Recchia (GPMAI)	Vessel survey
2010	Brazil/BA	Bianca Morais (GPMAI)	Vessel survey
2013	French Guiana/all along the coast	Laurent Kelle (WWF)	Aerial survey
2013–2015	Brazil/BA, RJ, SC	Leonardo Wedekin	Vessel survey
2014	Colombia/Atlantic, Magdalena	Fernando Trujillo (Fundación Omacha)	Vessel survey
2014 and 2015	Brazil/BA	Gabrielle Amorim (GPMAI)	Vessel survey
2015	Brazil/SP	Marcio Silva Bezzi	Vessel survey

Table 2.—Results obtained in the correlation analysis (factorial analysis) among a set of environmental variables according to factors MR1, MR2, MR3, and MR4. SST = sea surface temperature; SSS = sea surface salinity. Notation: The variables chosen for modeling are underlined. Variables: mean annual SSS, minimum monthly SSS, and maximum monthly SSS correspond to the first factor (MR1). Variables: rate of annual variation in salinity and annual variance of salinity correspond to the second factor (MR2). Variables: rate of annual variation in temperature of the ocean surface and annual variance of the temperature of the ocean surface correspond to the third factor (MR3). Variables: bathymetry, distance from the coast, bathymetric slope, and mean annual temperature of the ocean surface correspond to the fourth factor (MR4). The empty slots are results with values below 0.1.

Variables	MR1	MR2	MR3	MR4
Bathymetry (depth of the seafloor)	−0.189	0.154		0.474
Distance to shore				−0.523
Bathymetric slope				0.102
Mean annual SSS	0.958	−0.187		−0.203
Minimum monthly SSS	0.752	−0.578		−0.326
Maximum monthly SSS	0.992			
Annual range in SSS		0.932		0.412
Annual variance in SSS		0.852		
Mean annual SST	0.648	0.125	−0.171	0.381
Annual range in SST			0.977	
Annual variance in SST			0.966	0.152
	MR1	MR2	MR3	MR4
SS loadings	2.947	1.951	1.943	0.992
Proportion Var	0.268	0.177	0.177	0.09
Cumulative Var	0.268	0.445	0.622	0.712

their presence data, forming a circular or elliptic envelope in the environmental space (Carpenter et al. 1993). The algorithm therefore assumes that population growth rates of a species decline as the environment departs from the ecological optimum.

Another class of models is that of machine learning or artificial intelligence, such as those calculated by the MaxEnt (Phillips et al. 2006; Phillips and Dudík 2008; Elith et al. 2011) and SVM (Vapnik 2000; Guo et al. 2005; Drake et al. 2006; Lorena et al. 2011) algorithms. These models are different from the others because they adjust their functions using pseudo-absences that are randomly placed in the study area (background—Phillips et al. 2009; Lorena et al. 2011). To deal with the uncertainties related to different types of algorithms, an ensemble forecasting framework was used. This combined projection technique is used to provide a map of environmental suitability through the combination of different replicates generated by different algorithms where the total number of models is presented at each location of potential occurrence of the species (Araújo and New 2007).

Evaluation of the models.—For model evaluation, other occurrence points are used that are superimposed on the generated models. One method is to collect new data in the field or in the literature and contrast it with the previously generated models. However, because this was not possible in the present case, the bootstrap technique (Efron 1979) was chosen to evaluate the models after randomly dividing the data set into train (75% of the data to generate the models) and test data (25% of the data to validate the models—Guisan and Zimmermann 2000). The train points are compared with the generated models and two types of errors are calculated and described in a confusion matrix (Fielding and Bell 1997). Omission errors occur when the model excludes known presences and commission errors occur when model includes absences.

A decision threshold was established to transform the continuous distribution maps into categorical distribution maps (presence and absence—Fielding and Bell 1997) where, for example, regions with suitability equal to or greater than the threshold were predicted as potential regions for the occurrence of *S. guianensis*. Because our main objective was species evaluation to extinction risk, a cutoff value based on maximizing sensitivity + specificity (Maximized Sum Threshold—MST) was calculated using the “dismo” package. This maximizes the hits of presences and absences of the species more accurately (Manel et al. 2002; Jiménez-Valverde and Lobo 2007). Values equal to or greater than the highest sensitivity value therefore depicted areas suitable for the presence of Guiana dolphins. To evaluate the performance of the ENMs, the True Skill Statistics (TSS) metric was used to consider omission and commission errors: TSS is an index ranging from −1 to +1, where +1 equals perfect agreement and values of zero or less indicate a performance no better than random (Allouche et al. 2006). We followed the two recommendations of Barve et al. (2011) to select the background area for modeling by considering the potential historical dispersion and the current known distribution of the species.

Modeling.—Modeling was repeated 15 times for each algorithm, totaling 75 models (15 replicas × 5 algorithms = 75 models). The 15 replicas of each algorithm were combined through an ensemble approach to predict a consensus map of species potential distribution (Araújo and New 2007). After this procedure, a further combination was carried out of the five ensembles obtained by the algorithm, resulting in a combined potential geographical distribution map for the Guiana dolphin.

Results

Occurrence data.—A total of 859 points of occurrence of Guiana dolphins (Fig. 1) were used from Colombia to South Brazil whereby, after rarefaction, 99 points remained for use in the analyses (Fig. 2). We inform on this figure the number of research papers on Guiana dolphins (n = 139) per study area.

Environmental data.—A factorial analysis (Table 2) enabled selection of seven of the 11 environmental variables available on MARSPEC for modeling: bathymetry, distance to shore, bathymetric slope, SSS (minimum monthly and annual range), and SST (mean annual and annual range).

Modeling.—A consensus map of potential geographic distribution of the Guiana dolphin for the Neotropical region generated from modeling is presented in Fig. 3. Maps obtained with each algorithm (Bioclim, Gower, Mahalanobis, SVM, and MaxEnt) are presented as Supplementary Data SD1–SD5. The Supplementary Data SD6 details the evaluations of each model. TSS and AUC values are close to 1, suggesting good predictions were obtained each of the 15 replicates.

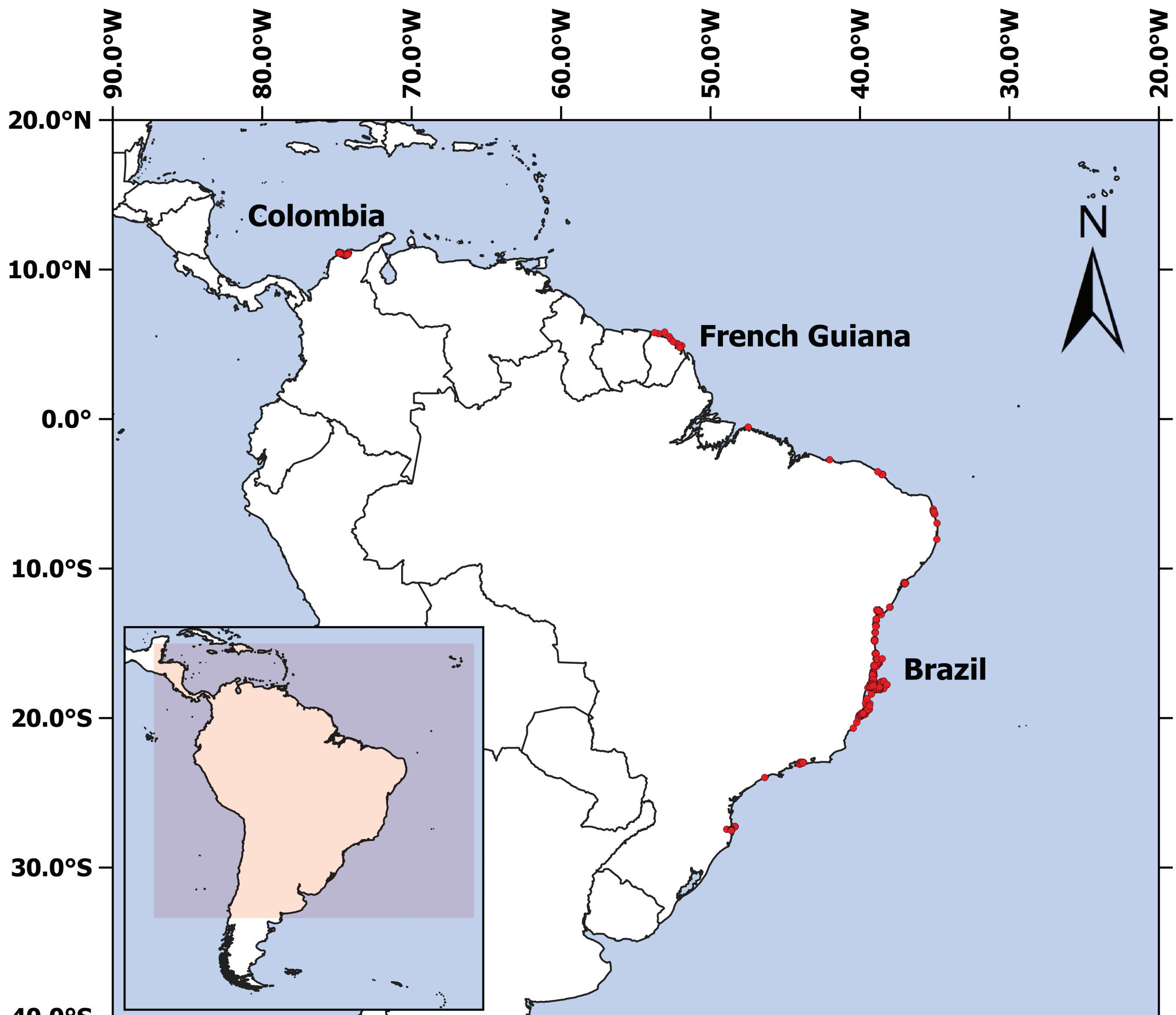

Fig. 1.—Map of 859 occurrence points of *Sotalia guianensis* in the Neotropical region.

The map shows high environmental suitability for the occurrence of the Guiana dolphin on the shallow regions of the continental shelf of South and Central America of the Atlantic Ocean. Furthermore, its potential distribution was demonstrated in regions of the Pacific Ocean, in colder waters of the South Atlantic Ocean, and islands where the species does not occur, such as in the Caribbean Sea, where the map demonstrates high environmental suitability.

Discussion

The known distribution area for the Guiana dolphin ranges from southern Brazil (Simões-Lopes 1988) to Nicaragua (Edwards and Schnell 2001) and probably Honduras (Evans and Davidson 2002). Within the known range, distribution usually is summarized by a polygon covering all continental shelf along its range with a fixed width (Flores and Da Silva 2009; Da Silva et al. 2010; Secchi et al. 2018). The models presented here, however, indicate a more heterogeneous distribution, more restricted to nearshore waters. This more restricted distribution is notable in regions with narrow continental shelves, such as Northeastern Brazil. The potential geographic distribution described by the models corroborates the vision proposed by some authors that the Guiana dolphin may be a habitat specialist whose ecological niche consists of a narrow coastal strip of shallow water (Wedekin et al. 2010). The clinal distribution with heterogeneous suitability along the coast, and the limited ability for dispersal (such as crossing deep stretches of sea and the Amazon plume) of the species, result in a structuration of populations along the Atlantic continental margin of the Central and South America (Cunha et al. 2011; Caballero et al. 2018). The longest known distance travelled by Guiana dolphins is 135 km and corresponds to three individuals that migrated between two adjacent bays (Santos et al. 2019).

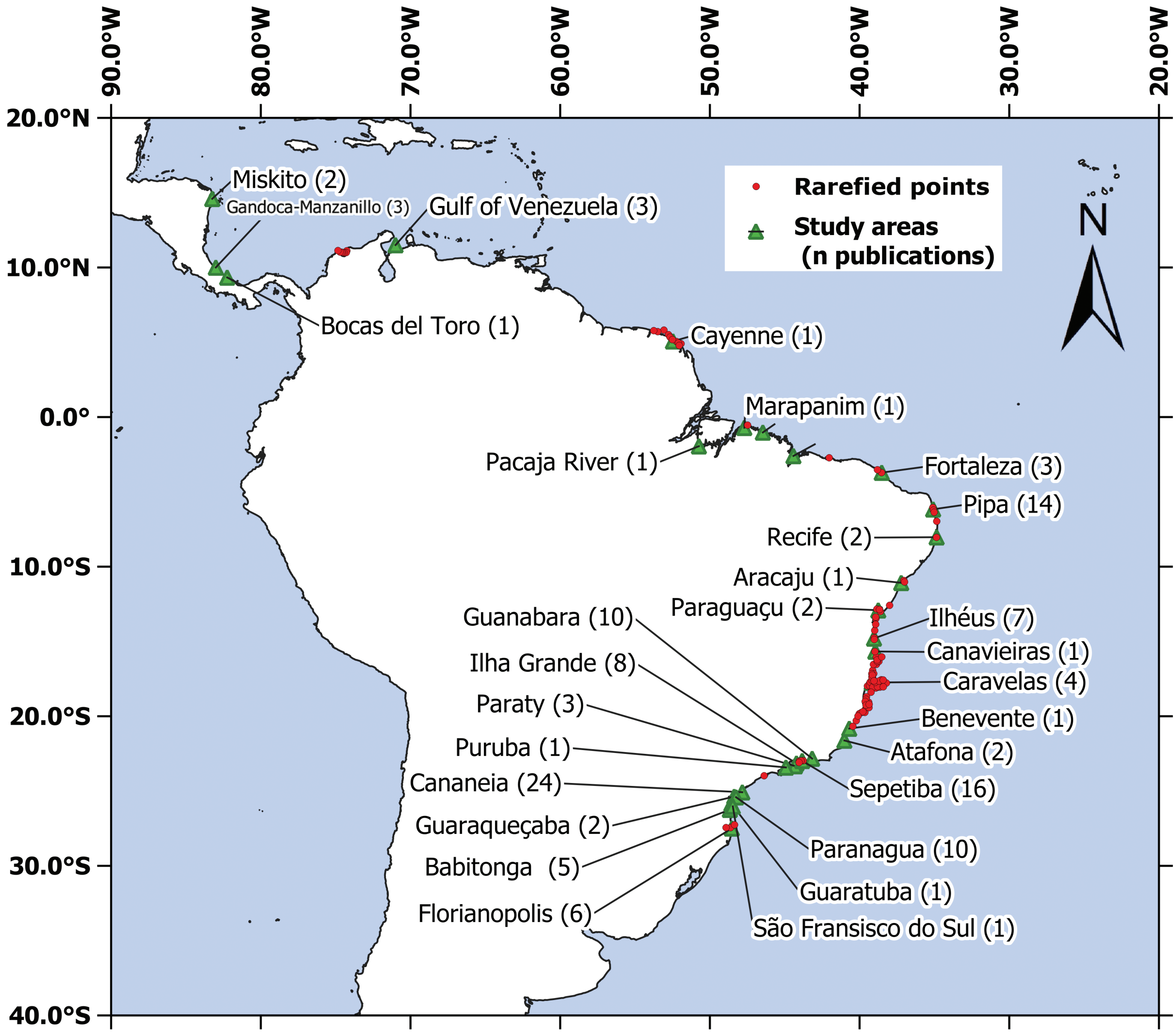

Fig. 2.—Map of 99 occurrence points of *Sotalia guianensis* after rarefaction in the Neotropical region and geographical distribution of the surveyed populations of *Sotalia guianensis*. The number of published articles for each study area is in brackets (see text for methodological details).

The ENMs calculated in the present study indicate potential areas for the distribution of *S. guianensis* in locations where there are no records of the species, such as areas of the Pacific Ocean, the Gulf of California, the Gulf of Mexico, Belize, and oceanic islands in the Caribbean Sea. We suggest that the absence of *S. guianensis* in these regions may be due to geographical (e.g., linking of North and South America), physical (e.g., water salinity and temperature), and biological (e.g., competition, limited ability to dispersal) limiting factors.

Recent studies indicate that North and South America probably joined between 10 and 15 million years ago (Bacon et al. 2015; Montes et al. 2015). This hypothesis is corroborated by the results found in the present study on the absence of Guiana dolphin in the Pacific Ocean, bearing in mind that the genus *Sotalia* only appeared 5 Ma ago (Cunha et al. 2005). The separation between marine and Amazonian species of *Sotalia* occurred approximately 2.3 Ma ago (Cunha et al. 2011) when the modern Amazon basin was established (Campbell et al. 2006; Figueiredo et al. 2009). Furthermore, according to Cunha et al. (2011), colonization of the Amazon basin by *Sotalia* certainly originated from the Atlantic, as the connection with the Caribbean was closed by the Andes around 8 Ma ago (Hoorn et al. 1995). We also suggest that animals were not able to reach the Pacific Ocean through the southern region of the Atlantic Ocean because there was no continuity of suitable habitats. Fewer than 10 models found potential areas for the occurrence of the species in the colder waters of Patagonia.

In the regions of the Gulf of Mexico, the islands of the Caribbean Sea (e.g., Grenada to the Virgin Islands, Puerto Rico, Dominican Republic, Bahamas, Cuba, Jamaica), a large part of the models (more than 50) found potential areas for the occurrence of the Guiana dolphin, despite there being no

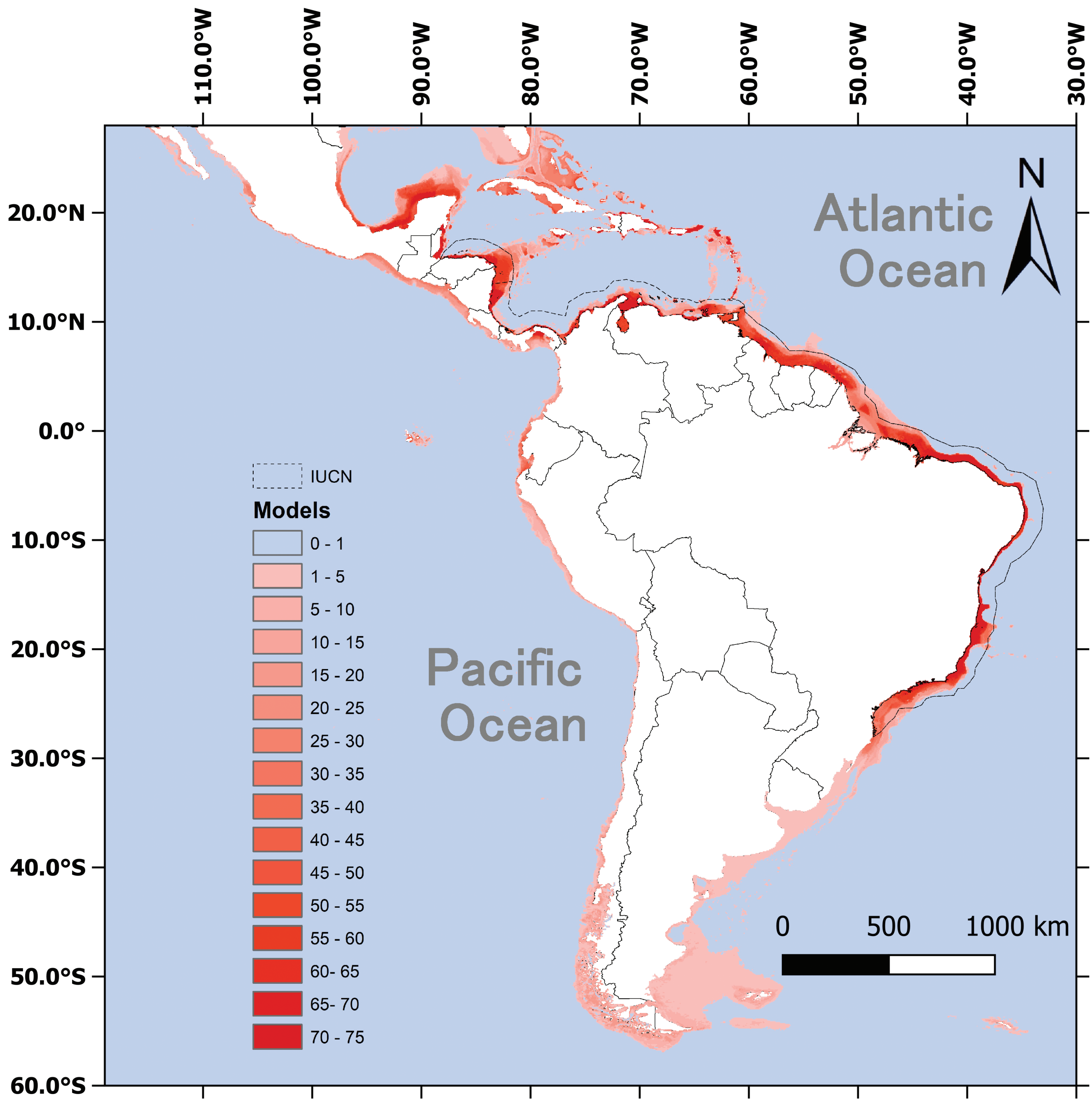

Fig. 3.—Map with the potential distribution of *Sotalia guianensis*, based on 75 ecological niche models. The intensity of the red tone increases as more models find environmental suitability for the occurrence of the species. The dotted area is the known distribution region of the species according to IUCN (Secchi et al. 2018).

knowledge of the presence of the species in these locations. In the case of the Caribbean islands, the deep regions that separate the islands represent discontinuities of the preferential habitats of the Guiana dolphin and may act as a type of behavioral dispersion barrier. Guiana dolphins occupy shallow areas at depths of up to 50 m, but generally less than 10 m (Azevedo et al. 2007; Da Silva et al. 2010; Tardin et al. 2020), except in some estuaries that they use intensively and cross deeper channels, up to 30 m (e.g., Batista et al. 2014; Godoy et al. 2015).

Other variables not included in the modeling also may be important for distribution of the species. The geographic distribution of the Guiana dolphin coincides with the distribution of mangrove ecosystems (Monteiro-Filho and Monteiro 2008). Association of Guiana dolphins with river estuaries also has been proposed (Rossi-Santos et al. 2006). Rivers and mangroves both may generate increased primary productivity and/or act as nurseries for different prey of the Guiana dolphin. The role of these and other habitat variables in the distribution of the species is worthy of being investigated in the future.

Another important factor that may preclude the establishment of the Guiana dolphin in certain areas is the presence of potential competitors or aggressors, such as the bottlenose dolphin, *Tursiops truncatus*. A larger species like the bottlenose dolphin can restrict the occurrence of the Guiana dolphin due to a possible negative interspecific interactions such as interference competition.

Agonistic behavioral interactions between bottlenose and Guiana dolphins were observed in captivity (Terry 1984) and in a natural environment in Brazil, at the southern limit of its distribution (Wedekin et al. 2004). The authors hypothesized that the large cohesive group observed in this region is a behavioral response to the imminent risk of aggressive interactions with bottlenose dolphins (Wedekin et al. 2004). Competition and interspecific aggressive interactions between these species also could influence the distribution of Guiana dolphins at their southernmost limit (Flores and Fontoura 2006). The southernmost 200 km of the Guiana dolphin's range corresponds to the area of overlap between two parapatric subspecies of bottlenose dolphin: the offshore subspecies *Tursiops truncatus truncatus* also is found to the north of this area while only the coastal subspecies (*T. truncatus gephyreus*) is present in shallow waters (< 20 m) south of this area (Simões-Lopes et al. 2019). Resident populations of coastal bottlenose dolphins occur in the Laguna complex and Lagoa dos Patos, two estuarine areas located, respectively, 50 and 500 km from the southern limit of the range of Guiana dolphin (Fruet et al. 2011; Daura-Jorge et al. 2012). Wedekin et al. (2004) reported an aggressive interaction of at least two hours between bottlenose and Guiana dolphins that occurred near the southern limit of the range of the Guiana dolphin. During this interaction, a calf of Guiana dolphin was repeatedly subjected to aggression and chased by three bottlenose dolphins although about 20 Guiana dolphins were close by. According to Shane (1995), aggressive interactions may lead to displacement and competitive exclusion of species that inhabit areas with limited food resources. The existence of populations of resident and transient coastal bottlenose dolphins in Belize (Kerr et al. 2005; Ramos et al. 2016) may partially explain the actual northern limit of the range of Guiana dolphins.

The absence of Guiana dolphins in regions considered suitable for the species by the ENMs corresponds to true (overprediction, e.g., cold waters of the South Atlantic Ocean) and apparent commission errors (Anderson et al. 2003). Apparent commission error can be due to competition with other species that restrict the distribution of the species (e.g., with the botlenose dolphin, as explained above) or to the lack of verification of the presence of the species in certain areas, an unlikely error given the coastal habit of the Guiana dolphin.

Thus, the models suggested potential areas for the occurrence of Guiana dolphins in areas where the species has never been recorded and is probably not present. An advantage of this type of error is that it reduces the likelihood of erroneously excluding areas of occurrence of the species, thereby maximizing their conservation efforts. In contrast, omission errors cause the models to overlook the presence of the species, even when the species is found to be present. This type of error can hamper the conservation of the species, because places where they are found would not be investigated. However, commission and omission errors can be minimized in accordance with the choice of decision threshold. In the present study, we used the criteria of maximum sensitivity and specificity threshold (MST), which supplies more accurate predictions (Jiménez-Valverde and Lobo 2007).

The points of occurrence used come from Brazil, French Guiana, and Colombia, at different densities. This sampling bias can affect the statistical analyses and models obtained. Although the rarefaction of the occurrence points enables the reduction of such biases, a nonsystematic sample does not suitably inform the ecological preferences of the species. However, spatial biases are difficult to avoid, because some regions are much more studied than others and have more occurrences than others. Nevertheless, an advantage of ENMs is their ability to predict a potential distribution of species through the relationship between their geographical coordinates (presence points) and available environmental characteristics (Peterson et al. 2011). Most of the areas determined by the models to be appropriate are within the known range of the species, suggesting good model accuracy. The areas that the models inferred to be environmentally suitable are potential areas of occurrence not yet known.

Based on the maps generated by the niche modeling studies, research efforts could better be applied. For example, researchers could use suitability maps to direct their studies to areas where models indicate a high probability of occurrence of the species (Fig. 3) but where little research has been done (Fig. 2). Accordingly, we suggest that some areas should be investigated as a matter of priority, such as the Caribbean off northern South America.

Ecological niche models do not reflect the effects of dispersion or biotic interactions, and as such, do not demonstrate a distribution of animals that is faithful to reality. The models generated in this project corroborate most of the known distribution of the Guiana dolphin, but suggests that biological factors, such as the presence of other species of coastal dolphins, may be important limiting factors for the Guiana dolphin at northern and southern extremes of its distribution. Furthermore, the potential distribution shown here can be used as a support tool for future research in the areas identified and suggested as being suitable for the occurrence of the species. One way of putting this technique into practice is to use the generated maps as a tool for strategy development by administrators and researchers, helping, for example, in the definition of areas to be investigated in order to maximize the efficiency of effort.

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Potential geographical distribution map of *Sotalia guianensis* based on the combination of 15 replicates of the Bioclim algorithm. The intensity of the red tone increases as more models find environmental suitability for the occurrence of the species. The dotted area is the known distribution region of the species according to IUCN (Secchi et al. 2018).

Supplementary Data SD2.—Potential geographical distribution map of *Sotalia guianensis* based on the combination of 15 replicates of the Gower algorithm. The intensity of the red tone increases as more models find environmental suitability for the occurrence of the species. The dotted area is the known distribution region of the species according to IUCN (Secchi et al. 2018).

Supplementary Data SD3.—Potential geographical distribution map of *Sotalia guianensis* based on the combination of 15 replicates of the Mahalanobis algorithm. The intensity of the red tone increases as more models find environmental suitability for the occurrence of the species. The dotted area is the known distribution region of the species according to IUCN (Secchi et al. 2018).

Supplementary Data SD4.—Potential geographical distribution map of *Sotalia guianensis* based on the combination of 15 replicates of the Support Vector Machines (SVM) algorithm. The intensity of the red tone increases as more models find environmental suitability for the occurrence of the species. The dotted area is the known distribution region of the species according to IUCN (Secchi et al. 2018).

Supplementary Data SD5.—Potential geographical distribution map of *Sotalia guianensis* based on the combination of 15 replicates of the Maximum Entropy (MaxEnt) algorithm. The intensity of the red tone increases as more models find environmental suitability for the occurrence of the species. The dotted area is the known distribution region of the species according to IUCN (Secchi et al. 2018).

Supplementary Data SD6.—Results from the evaluations of the 15 replicates of the models: Bioclim, Gower, Mahalanobis, Support Vector Machines (SVM), and Maximum Entropy (MaxEnt). Note: Evaluation metrics in bold: AUC (ROC—Receiver Operating Characteristic) and TSS (True Skill Statistics).

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