

# Not going with the flow: Ecological niche of a migratory seabird, the South American Tern *Sterna hirundinacea*

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## ARTICLE INFO

### Keywords:

Coastal provinces  
Migration  
Niche overlap  
Niche divergence  
Niche truncation  
Seasonality

## ABSTRACT

Defining a species' ecological niche is not a trivial task particularly for marine taxa, since physical and biological constraints are not easily perceived in these environments. Yet, coastal habitats are divided into provinces, influenced by different environmental conditions, such as superficial marine currents, causing seasonality in marine productivity and biomass. The South American Tern *Sterna hirundinacea* is a poorly known, migratory seabird distributed along the Pacific and Atlantic coasts of South America, including the Malvinas/Falkland Islands, and occurring in most of the South American coastal provinces. Limited knowledge on the migratory behaviour of the species points to differential habits between southern and northern populations. The species' breeding season also varies with latitude and season, occurring during spring in the south and in the fall in northern areas of the species occurrence. These observations point to putatively ecologically distinct populations along the species range that seem to be coincident with coastal provinces. To test our hypotheses, we estimated full-range ecological niche models per season, and we used coastal provinces to model ecological niches for each of the known breeding areas/seasons. We also tested for environmental space differentiation between seasons and breeding and non-breeding areas. Overall, the species does not seem to occupy significantly different ecological niches throughout the year, except during the breeding season, particularly between the Warm Temperate Southeastern Pacific and Warm Temperate Southwestern Atlantic provinces in fall. This suggests that the South American Tern migratory behaviour, the selection of different microhabitats and reproductive areas or distinct biological interactors might be influencing the species environmental space. Nonetheless, our models reinforce the gradual migration of this tern species towards the south, spending the summer mostly in the Malvinas/Falkland Islands. Interestingly, the species seems to be resident in Peru coastal area. Thus, despite the absence of ecological divergence, population structure should be tested and demographic trends assessed along the species range.

## 1. Introduction

The concept of niche is one of the most relevant in ecology, yet one of the most discussed and difficult to apply in practice (e.g., Brown and Carnaval, 2019; Peterson and Soberón, 2012). Multiple concepts have been suggested, from the arguably simplest fundamental niche, comprising the set of environmental combinations in which viable populations can persist to promote the survival of the species (Peterson et al., 2011), to the more complex definition of occupied niche, which further considers biological interactors (e.g. pollinators, dispersers, competitors, and predators) and the accessible areas for population dispersal (Barve et al., 2011; Peterson et al., 2011; Soberón et al., 2017).

However, most of these biotic factors are difficult to represent in the niche modelling process, hence are rarely included (Barve et al., 2011; Soberón et al., 2017). Moreover, in real-life situations, species are in a non-equilibrium state, i.e., over ecological times, their distribution ranges are constantly shifting in response to biotic interactions, the appearance of geographic barriers, seasonal climatic patterns and other anthropogenic disturbances (Araújo and Pearson, 2005; Brown and Carnaval, 2019; Elith et al., 2010; Eyres et al., 2017; Peterson and Soberón, 2012).

In this regard, several studies have also emphasized the importance of selecting appropriate calibration areas to build ecological niche models (ENMs) that provide the most ecologically realistic results, i.e.,

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<https://doi.org/10.1016/j.ecolmodel.2021.109804>

Received 19 February 2021; Received in revised form 29 October 2021; Accepted 30 October 2021

Available online 8 November 2021

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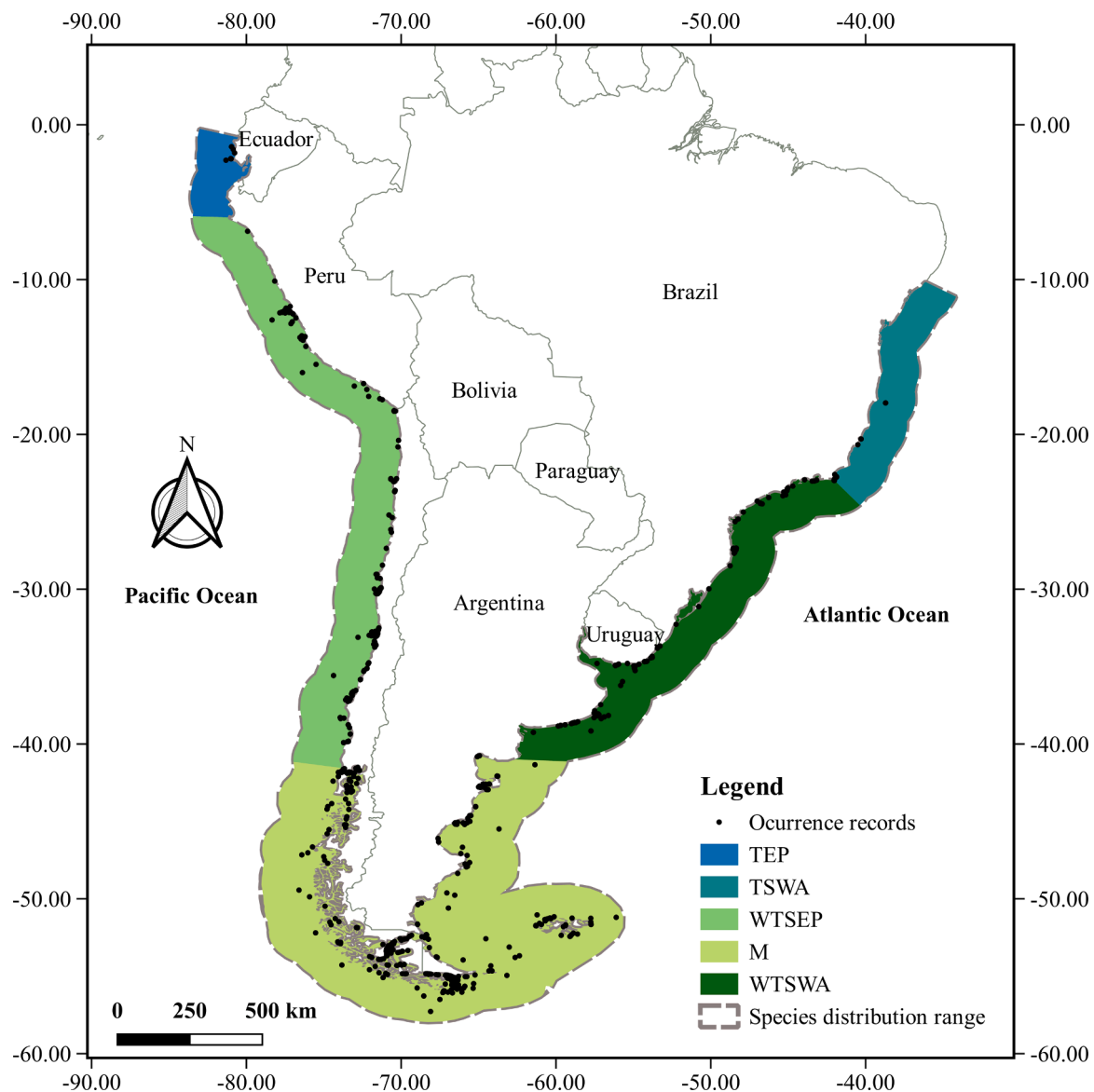
choosing areas large enough to consider the species mobility, but restricted enough to reflect their dispersal limitations (Anderson and Raza, 2010; Barve et al., 2011; Giovanelli et al., 2010; Peterson, 2011; Soberón and Peterson, 2005; VanDerWal et al., 2009). While this selection might be straightforward in terrestrial environments, where physical (e.g. rivers, mountains) and biological barriers (e.g. competitors) are often easily perceived (Azuaje-Rodríguez et al., 2020; Tocchio et al., 2015), modelling marine species is a particular challenge, especially for migratory species, due to the lack of evident barriers to dispersal (Melo-Merino et al., 2020) and limited knowledge on migration habits and data for non-breeding areas (Ponti et al., 2020).

Understanding ecological requirements and distribution of seabirds is vital for their conservation and the maintenance of their ecosystems, since seabirds are top predators in the marine environments, and their populations act as bioindicators of oceanographic changes, responding to the increase in the sea surface temperature (Weimerskirch et al., 2003). Direct disturbances on marine natural habitats are affecting both the migratory behaviour and the survival of these birds (Dias et al., 2019; Hogan et al., 2010; Russell et al., 2015; Senner et al., 2017; Yorio

et al., 1994). So far, although seabirds are globally spread, studies assessing their seasonal distributions and ecological requirements have been mostly conducted in the Atlantic coasts (Melo-Merino et al., 2020). Models with high temporal and spatial resolution are still lacking for most of the South American species, particularly those occurring in the Pacific coasts (Melo-Merino et al., 2020). Therefore, how southern coastal environments shape the seabirds' migratory behaviour and influence population differentiation have been seldom addressed topics (but see, e.g. Ingenloff, 2017; Scales et al., 2016).

Along marine coasts, different superficial marine currents increase productivity and biomass heterogeneously, creating distinct feeding areas for seabird communities (Bost et al., 2009; Friedlaender et al., 2011), and possibly forcing populations to vary their migratory and reproductive habits according to the food availability (Bost et al., 2009). These areas harbour different sets of endemic taxa, and have been divided into provinces to convey such marine variability (Spalding et al., 2007).

In South America, provinces from the Atlantic coast, Tropical Southwestern Atlantic and Warm Temperate Southwestern Atlantic



**Fig. 1.** Calibration area for the South America Tern *Sterna hirundinacea* models and distribution of the occurrence records used. coloured areas represent coastal provinces following the global biogeographic system for coastal and shelf areas, marine regions of the world (Spalding et al., 2007): warm temperate Southwestern Atlantic (WTSWA), Magellanic (M), warm temperate Southeastern Pacific (WTSEP), tropical Eastern Pacific (TEP) and the tropical Southeastern Atlantic (TSWA).

(Fig. 1), present an enhanced marine productivity resulting from superficial marine currents from the subtropical surface warm water of Brazil and sub-Antarctic cold waters from the Antarctic Circumpolar current (Olson et al., 1988; Spalding et al., 2007). In the Pacific coast, the Tropical Eastern Pacific and Warm Temperate Southeastern Pacific provinces are influenced by the cold, nutrient-rich water from the Humboldt Current System and the Antarctic Polar front (Spalding et al., 2007; Thiel et al., 2007; Weichler et al., 2004). Lastly, the most southern province, the Magellanic Province, is characterized by low water salinity, cold temperatures, and high concentration of nutrients product of the convergence of the sub-Antarctic and Antarctic polar fronts and the Malvinas/Falkland Current (Olson et al., 1988; Spalding et al., 2007).

The South American Tern, *Sterna hirundinacea*, is a migratory seabird restricted to a narrow coastal area within the Atlantic coast, mostly from the south of Brazil to Argentina, including the Malvinas/Falkland Islands, and in the Pacific coast, from Chile to Peru (Fig. 1). In austral winter, the species distribution occasionally extends further north to Ecuador and north-eastern of Brazil, but resident populations seem to be established in the rest of the territory (Gochfeld et al., 2020), making this species to occur in the majority of the South American coastal provinces (Fig. 1). The South American Tern southern populations seem to present a long-distance directional migration, making long distance seasonal movements along Chilean coasts, and Argentina and Malvinas/Falkland Islands (Eyres et al., 2017; Gochfeld et al., 2020). However, it is uncertain if long-distance migrations are also performed by the South American Tern connecting both northern and southern populations. This observation might suggest the delimitation of distinct populations for the South American Tern along latitudinal and longitudinal axes, i.e., Pacific vs. Atlantic and northern vs. southern populations. Furthermore, the breeding season varies markedly with latitude, reproduction occurs during spring (from October to December) for southern breeding colonies distributed on the coast of Southern Argentina and Chile, and the Malvinas/Falkland Islands (i.e., mostly in the Magellanic Province; Fig. 1; Carlos, 2009; Gochfeld et al., 2020; Portflitt-Toro et al., 2018). Whereas, northern breeding colonies are established in the fall (between April and June), being distributed along the coast of Brazil (corresponding to the Warm Temperate Southwestern Atlantic Province; Fig. 1), and north of Chile and Peru (i.e., within the Warm Temperate Southeastern Pacific Province; Fig. 1; Carlos, 2009; Gochfeld et al., 2020; Portflitt-Toro et al., 2018; Vooren and Chiaradia, 1990).

Thus, the putatively different migratory behaviour and particularly the different seasonally reproductive habits along the species distribution suggest the South American Tern might harbour ecologically distinct populations, limited by the South American coastal provinces (Fig. 1). In this context, here we use this tern species to test the utility of coastal provinces delimitation in the niche modelling procedure for seabirds by i) estimating ENMs for the entire range of distribution of the South American Tern per season, and in each of the putative breeding populations delimited by coastal provinces, ii) by comparing ecological niches between breeding and non-breeding areas and seasons, through environmental space differentiation testing, and iii) by describing the most relevant environmental variables that influence the species distribution.

## 2. Material and methods

### 2.1. Occurrence data

The study area includes the Atlantic (latitude from  $-9.8^{\circ}\text{N}$  to  $-58.6^{\circ}\text{S}$  and longitude from  $-69.4^{\circ}\text{W}$  to  $-33.3^{\circ}\text{E}$ ) and the Pacific coasts of South America (latitude from  $-0.14^{\circ}\text{N}$  to  $-58.01^{\circ}\text{S}$  and longitude from  $-84.2^{\circ}\text{W}$  to  $-67.1^{\circ}\text{E}$ ). We delineated calibration areas as coastal marine areas within a 250 km buffer around the shore (Fig. 1), considering the South American Tern mobility, the maximum distance from

shore to high sea observed from the species' occurrence records and the distance between mainland and the Malvinas/Falkland Islands (Barve et al., 2011; Gochfeld et al., 2020; Ingenloff, 2017; Soberón and Peterson, 2005). We used the QGIS platform v. 2.18.28 to delineate the study area (QGIS Development Team, 2019). We collected 8585 occurrence records for the South American Tern from online repositories: VertNet (vertnet.org, accessed January 2019), Xeno-canto (xeno-canto.org, accessed January 2019), and Global Biodiversity Information Facility (gbif.org, accessed July 2019), corresponding to the period between 1907 and 2019. These repositories present a data quality control and expert review before the online publication. We removed records with incomplete geographic information, duplicated records from the same grid square, and records falling outside the calibration area using the package 'modelos' in R v. 3.5.3 (R Core Team, 2019). We used a final dataset of 644 occurrence records (Fig. 1; Table S1), and divided these records according to the Southern Hemisphere meteorological seasons: Spring (September 21–December 20), Summer (December 21–March 20), Fall (March 21–June 20) and Winter (June 21–September 20) to accommodate the species reproductive and migratory seasonality into the ENMs (Eyres et al., 2017; Ingenloff, 2017; NASA OceanColor Web, 2019). Even though the records extended over a 112-years period, most of them were collected in the last few years (Fig. S1). In addition, exploratory analyses dividing the records into old (1907–2001) and modern datasets (2002–2019) revealed similarity in the environmental and geographic spaces between sets, supporting all records could be used in the modelling procedure.

### 2.2. Environmental data

We used eight environmental variables known to be ecologically relevant for seabirds (Barrett and Krasnov, 1996; Weichler et al., 2004). We obtained the following variables from global MODIS Aqua L3 SMI data: absorption coefficient due to phytoplankton at 443 nm, chlorophyll-a concentration, photosynthetically available radiation, particulate organic carbon, particulate inorganic carbon, sea surface temperature, nightly sea surface temperature, and diffuse attenuation coefficient (oceancolor.gsfc.nasa.gov, accessed August 2019). These environmental variables encompassed seasonal climatology mean composite and were downloaded separately for each season. The variables corresponded to the period between 2002 and 2019, and presented a 4 km spatial resolution to match the resolution of the occurrence data (Franklin, 2010; Peterson et al., 2011). To select from these eight environmental variables those uncorrelated for the modelling procedure, we performed a Pearson's correlation analysis using the 'usdm' R package, considering a correlation threshold  $r < 0.70$  (Dormann et al., 2013; R Core Team, 2019; Zar, 1999).

### 2.3. Ecological niche modelling

Since enough evidence exists for ecological seasonality in the South American Tern (i.e., migration occurring mostly during the winter and summer, and reproduction during the spring and fall; Carlos, 2009; Eyres et al., 2017; Gochfeld et al., 2020; Portflitt-Toro et al., 2018), we completed ENMs by season, following two different approaches. In the first approach, we calibrated models for the entire species distribution range, with no delimitation of geographic populations, resulting in four ENMs (i.e., one per season). For the second approach, we calibrated ENMs for the three known breeding areas/seasons for the South American Tern, considering their delimitation by the coastal provinces from the Global Biogeographic System for Coastal and Shelf Areas, Marine Regions of the World (Spalding et al., 2007): Magellanic Province in the spring, Warm Temperate Southeastern Pacific, and Warm Temperate Southwestern Atlantic Provinces in the fall (Fig. 1), and then performed projections into the entire species distribution range. We expected to obtain higher occurrence probability within provinces during breeding seasons, if the environmental features of the coastal provinces would be

good proxies to delimit ecologically distinct populations of the South American Tern.

We selected Maxent, a presence-background algorithm, because we only had presence records for the South American Tern, and such algorithms are considered less biased than absence-based methods in such cases (Peterson et al., 2011). We ran the algorithm in the 'kuenm' package in R v. 3.5.3 (Cobos et al., 2019; R Core Team, 2019). This package allows species-specific settings to generate the ENMs, such as feature classes, standardized multiplier values and the use of different data partitioning methods. In addition, the package automates model calibration, evaluation and reproducibility (Cobos et al., 2019).

For each model, we performed 10 replicates with the bootstrap method, allowing for a random 75% training and 25% testing data partition. We generated 10,000 random background points throughout the entire calibration area (Phillips et al., 2009; Phillips and Dudík, 2008). Such random background method assumes that the species is equally likely to reach any location across the calibration area (Merow et al., 2013). To obtain the best model possible, in each replicate, we tested three feature classes ( $l$  = linear,  $q$  = quadratic,  $p$  = product) in three different combinations ("lq", "lp", "pq"), and five different standardized multiplier values (0.1, 0.25, 0.5, 1, 2, 4; Merow et al., 2013). To assess the significance of each model, we used the partial area ROC curve using 50% of random points and 500 bootstrap iterations, considering best models with mean  $\leq 1$  and  $p$ -value  $< 0.05$  (Peterson et al., 2008). The performance of each model was assessed through omission rates, with good performances corresponding to a rate  $\leq 5\%$  (Cobos et al., 2019). Finally, the Akaike's Information Criterion (AICc) was used to assess models complexity. AICc values close to zero were preferred (Muscarella et al., 2014). We used the complementary log-log (cloglog) transformation in Maxent to estimate the occurrence probability (Phillips et al., 2017). Finally, for the model projections under the second modelling approach, we used the free extrapolation setting, to predict the responses in the entire area of distribution of the species. The R code for all the methodological procedures and a brief description of the models following the ODMAP (Overview, Data, Model, Assessment, and Prediction) protocol (Zurell et al., 2020) are provided in the Appendix S1 and table S2.

## 2.4. Environmental space comparisons

We used the 'humboldt' package in R v. 3.5.3 (Brown and Carnaval, 2019; R Core Team, 2019) to test if the occupied niche for the South American Tern varies throughout the year and distribution range, i.e., between seasons and areas, respectively. This algorithm overcomes the need for similar geographical space between the target species/populations, allowing to compare different regions, and considers a multidimensional and abstract environmental space, accounting for the non-equilibrium state that characterizes wild species distributions (Brown and Carnaval, 2019; Warren et al., 2010, 2008).

We performed both the niche overlap test and the niche divergence test (Brown and Carnaval, 2019). These tests distinguish whether differences in the environmental-space emerge from true niche divergence or result from other factors (such as life-history traits, biological interactors or the configuration of the accessible environments; Brown and Carnaval, 2019). In each test, we considered Schoener's D niche similarity index (which ranges from 0 to 1, with 1 denoting complete overlap; Warren et al., 2008) and a statistical significance at  $P \leq 0.05$  for the equivalence and background statistics (Brown and Carnaval, 2019). A significant value ( $P \leq 0.05$ ) for the equivalence and background statistics in both niche overlap and divergence test indicates that the niches compared are different and divergent (Brown and Carnaval, 2019). In addition, we estimated the potential niche truncation index (PNTI) to evaluate if the species occupied niche reflects its fundamental niche (Brown and Carnaval, 2019), per season and province. Moderate ( $0.15 \leq \text{PNTI} \leq 0.3$ ) to high-risk values ( $\text{PNTI} > 0.3$ ) inform that the occupied niche does not match the fundamental niche of the species. To do so, we

removed occurrences closer than 50 km to each other to avoid spatial autocorrelation (rarefy.units = 50 km), reduced the input data so that the extent was identical (reduce.env = 2) and we used a Principal Component Analyses (reductype = PCA) to represent the environmental space. We also corrected the occurrence densities of each dataset (correct.env = T) and used a kernel smooth scale of 0.75 and values of kernel density of 0.0001 (thresh.space.z).

We first completed comparisons between seasons, considering the full distribution range of the South American Tern, to assess niche differentiation and divergence along the species annual migration. We expected to find niche similarity between seasons, justifying the migratory movement. Secondly, we tested variation between breeding areas/seasons (i.e., Magellanic Province during spring, and each of the Warm Temperate Southwestern Atlantic and the Warm Temperate Southeastern Pacific Provinces in fall) and non-breeding areas/seasons (i.e., all the other possible combinations between provinces and seasons) to detect niche differentiation and divergence during the species annual reproductive cycle. We expected to find niche differentiation between breeding and non-breeding areas/seasons, justifying the regionally asynchronous breeding periods.

## 3. Results

### 3.1. Ecological niche models (ENMs)

Four environmental variables were selected after Pearson's correlation test: chlorophyll-a concentration, absorption due to phytoplankton at 443 nm, particulate inorganic carbon, and sea surface temperature (see Fig. S2 for a detailed annual variation of each environmental variable).

The final dataset comprised 644 occurrence records for the South American Tern; the number of observations for the spring and summer (68.32%,  $n = 440$ ) was superior to that for the fall and winter (31.68%,  $n = 204$ ; Table 1). During breeding seasons, most of the records correspond to the Magellanic Province (18.2%,  $n = 117$ ), follow by the Warm Temperate Southeastern Pacific (6.52%,  $n = 42$ ) and the Warm Temperate Southwestern Atlantic (4.4%,  $n = 28$ ; Table 1). Importantly, we have found a limited number of occurrences during the breeding season within the Tropical Eastern Pacific ( $n = 2$ ) and the Tropical Southeastern Atlantic Provinces ( $n = 4$ ), with most of the occurrences in these provinces collected during the winter ( $n = 20$ ).

The parameters for each of the best models selected are depicted in Table 1. The partial area under the ROC curve values and the Akaike's Information Criterion supported statistical significance and good performance of all the ENMs (Table 1). In addition, omission rates values were overall low ( $\leq 0.07$ ; Table 1).

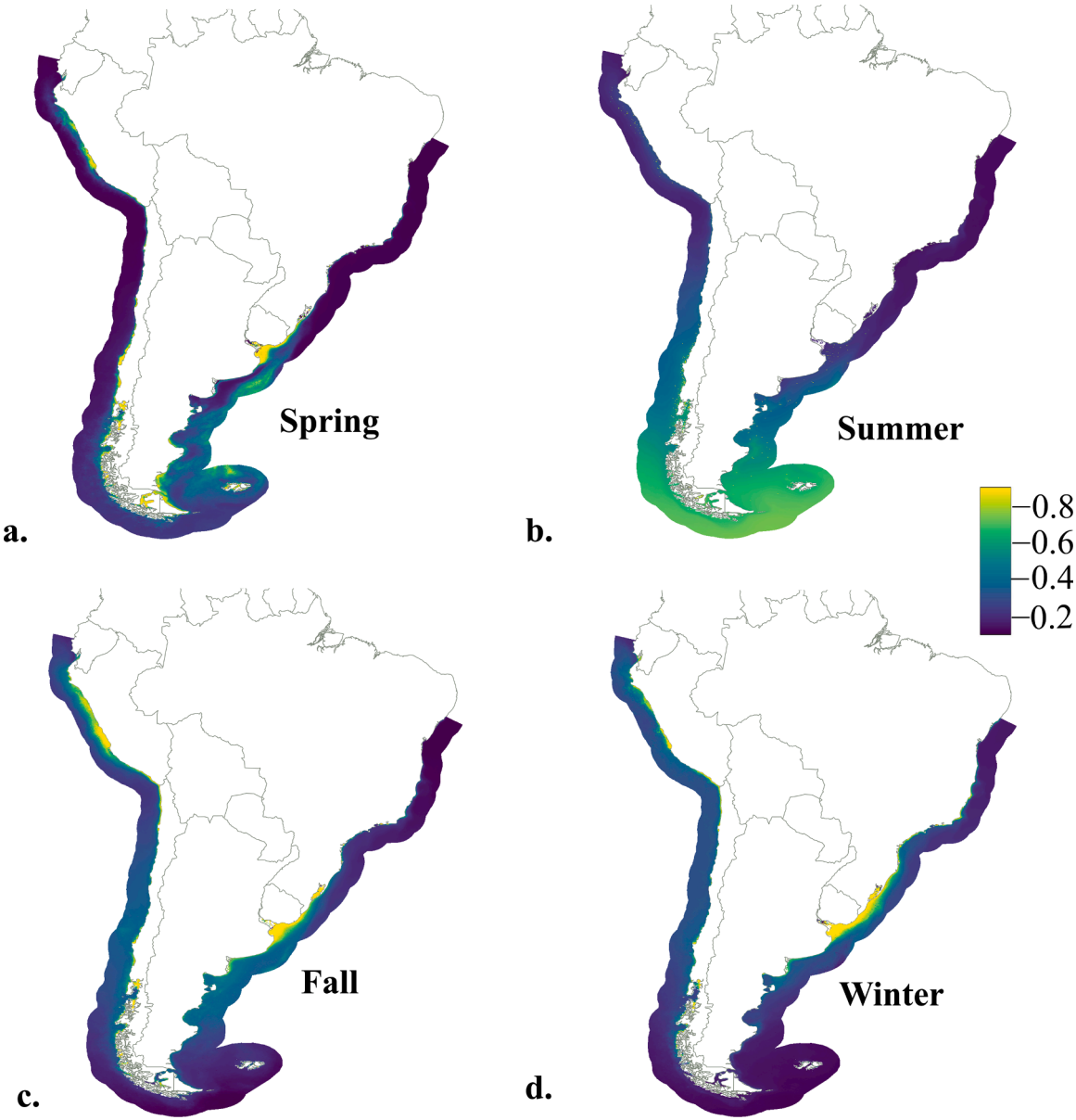
The occurrence probability obtained in the first modelling approach (Fig. 2) was ecologically realistic and gave a good representation of the migratory behaviour of the species (Fig. 2). In this first approach, the areas in the north were almost entirely replaced by southern locations from winter to summer, with the exception of Peru coastal area that remained with a high occurrence probability year-round (Fig. 2). In the second modelling approach, projections made for the fall within the Warm Temperate Southeastern Pacific Province (Fig. 3a,b) and spring in the Magellanic Province (Fig. 3c,d) predicted a high occurrence probability outside the known area of occurrence for the species in each time of the year. Only for the fall within the Warm Temperate Southwestern Atlantic Province, the projection supported higher occurrence probability within the reported breeding area (Fig. 3d,e).

Response curves for the first modelling approach indicated a positive correlation between the absorption coefficient due to phytoplankton at 443 nm and the occurrence probability of the species during the spring, but not so during the other seasons (Fig. S3 a, e, i, m). The chlorophyll-a concentration was also positively correlated with the occurrence probability of the species during all the seasons (Fig S3 b, f, j, and n). Conversely, the particulate inorganic carbon was negatively correlated



**Table 1**  
Statistics for the performance of the ecological niche models obtained. The calibration and projection areas, number of records (N), annual season, mean partial ROC scores (pROC), omission rates (OR), Akaike's information criteria (AICc), best feature classes (FC, *l* = linear, *q* = quadratic, *p* = product) and regularization multipliers (RM) for each model are informed.

Approach	Calibration area	Projection area	N	Season	Mean pROC	P value	OR	AICc	FC	RM
1	Entire species distribution range	-	204	Spring	1.36	0	0.02	0	lq	0.1
			236	Summer	1.25	0	0.07	0	q	1
			96	Fall	1.36	0	0.04	0	lq	0.25
			108	Winter	1.34	0	0.04	0	lq	0.25
2	Warm Temperate Southeastern Pacific	Entire species distribution range	42	Fall	1.27	0	0.03	0	q	1
	Magellanic	Entire species distribution range	117	Spring	1.20	0	0.03	0	lq	0.1
	Warm Temperate Southwestern Atlantic	Entire species distribution range	28	Fall	1.50	0	0	0	lq	0.1

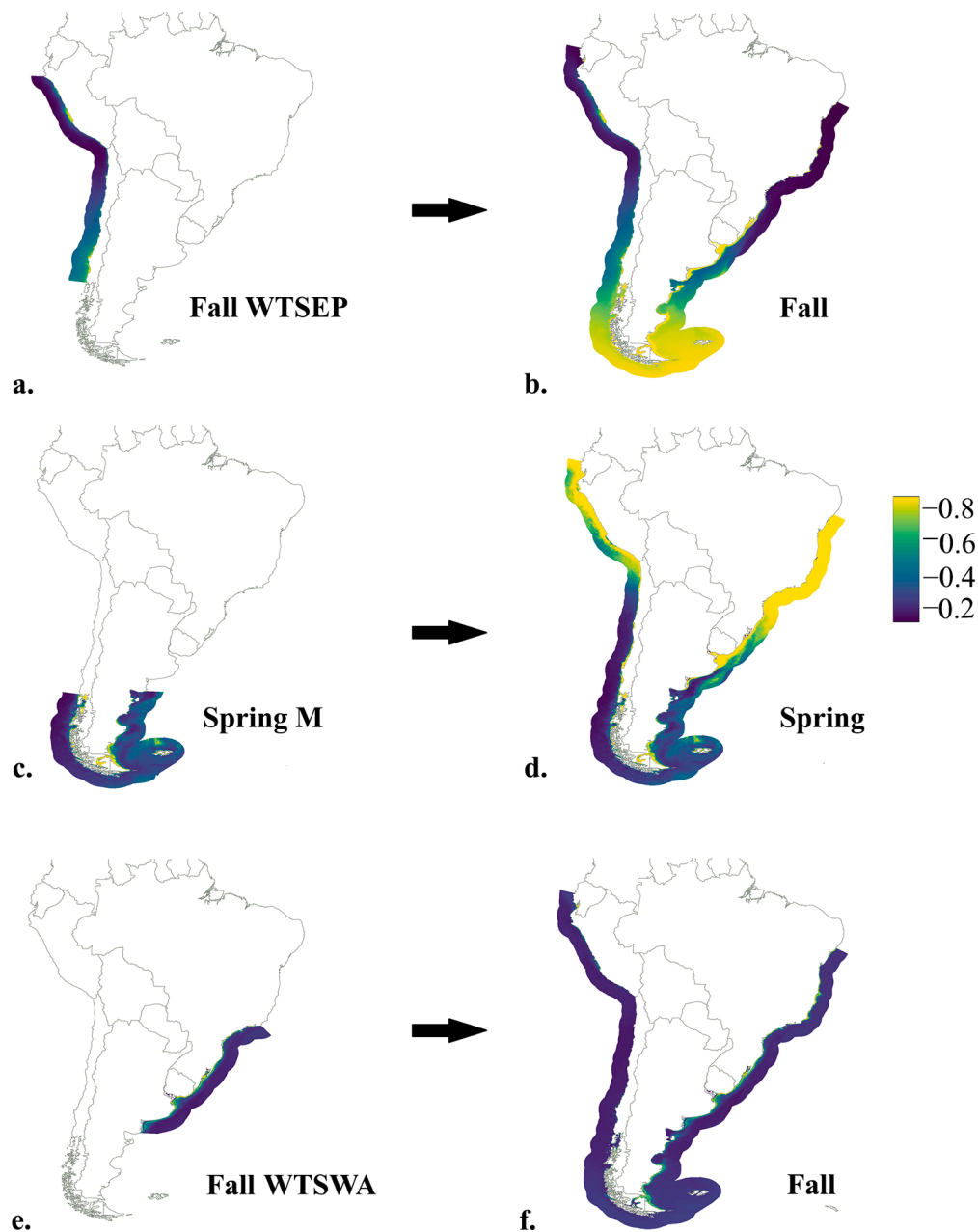


**Fig. 2.** Occurrence probability for the South America Tern *Sterna hirundinacea* under the first modelling approach: a. spring, b. summer, c. fall and d. winter.

with the species' occurrence during all but the summer season (Fig. S3 c, g, k, o). Similarly, during spring and summer, as the sea surface temperature increased, the occurrence probability of the species decreased (Fig S3 d, h).

3.2. Environmental space comparisons

The niche overlap tests between seasons considering the entire species distribution range ( $D \leq 0.19$ ;  $E > 0.05$ ) and in the provinces during non-breeding seasons ( $D \leq 0.09$ ;  $E > 0.05$ ) indicated niche equivalency (Table 2). Conversely, only one comparison between breeding seasons,



**Fig. 3.** Occurrence probability for the South America Tern *Sterna hirundinacea* projections using Maxent algorithm. The models were calibrated using records for each breeding area per season, and projected to the entire species distribution range. The three calibration areas corresponded to the Warm Temperate Southeastern Pacific (WTSEP; a-b), Magellanic (M; c-d) and Warm Temperate Southwestern Atlantic (WTSWA; c-e) provinces.

Warm Temperate Southeastern Pacific Province vs. Warm Temperate Southwestern Atlantic Province in fall, supported niche differentiation ( $D = 0.01$ ,  $E \leq 0.05$ ). The niche divergence tests supported no niche divergence in the shared analogous environments for the comparisons between seasons ( $D \leq 0.24$ ;  $E > 0.05$ ) and provinces during breeding and non-breeding seasons ( $D \leq 0.11$ ;  $E > 0.05$ ; Table 2). We were not able to perform some niche divergence tests between provinces due to little overlap in shared/analogous environments (Table 2). For the comparisons performed, analogous climate space percentage varied between 83% and 61% (Table 2). In all comparisons performed, at least one background statistic was non-significant, supporting the similarity of the compared niches (Brown and Carnaval 2019). All niche comparisons presented between low to moderate niche truncation ( $\text{PNTI} \leq 0.17$ ; Table 2). Niche comparisons between provinces resulted in variable levels of niche truncation (Table 2).

## 4. Discussion

### 4.1. The South American Tern ecological niche

The occurrence records we have gathered confirm that the South American Tern only occurs occasionally, during winter, in the northmost area of the species occurrence, i.e., within the Tropical Eastern Pacific and Tropical Southeastern Atlantic Provinces (Carlos, 2009; Gochfeld et al., 2020). General distribution patterns and seasonality previously documented for the South American Tern further supports the species winters mainly on the coasts of Brazil and Peru and spends the summer in Chile and Argentina (Bugoni and Vooren, 2005; Carlos, 2009; Gochfeld et al., 2020; Portflitt-Toro et al., 2018; Vooren and Chiaradia, 1990). This seasonal behaviour is well evidenced in the records available for the Atlantic, particularly southern Argentina, with considerably

**Table 2**

Environmental space comparisons between seasons and coastal marine provinces for the South American Tern *Sterna hirundinacea*. Niche overlap (NOT) and niche divergence (NDT) tests, Schoener's niche similarity index (D), equivalence statistic (E), background statistics (B), analogous climate space percentage (A), Potential Niche Truncation index (PNTI), number of records remained and used in each comparisons ( $N_r$ ), Warm Temperate Southwestern Atlantic (WTSWA), Magellanic (M), Warm Temperate Southeastern Pacific (WTSEP). \* $0.01 < p \leq 0.05$ ; \*\* $0.01 < p \leq 0.001$ ; \*\*\* $p < 0.001$ . (-) Comparisons with little overlap in shared/analogous environments, insufficient to perform the NDT.

Seasons and provinces				NOT				NDT				PNTI		
1	$N_r$	2	$N_r$	D	E	B <sub>1-2</sub>	B <sub>2-1</sub>	D	E	B <sub>1-2</sub>	B <sub>2-1</sub>	A	1	2
Spring	96	Summer	97	0	0.92	**	**	0.06	0.32	0.15	0.75	76.2	0.17	0.07
Spring	96	Fall	53	0.04	0.10	0.70	**	0.24	0.99	0.87	*	71.9	0.12	0.08
Spring	96	Winter	55	0.02	0.80	**	0.52	0.07	0.24	0.97	0.34	68.3	0.08	0.02
Summer	97	Fall	53	0.01	0.15	0.53	**	0.05	0.74	0.86	*	72.6	0.07	0.12
Summer	97	Winter	55	0.19	0.94	**	**	0.09	0.89	0.20	**	70.8	0.04	0.07
Fall	53	Winter	55	0.11	0.76	**	*	0.17	0.86	*	*	83.7	0.05	0.05
M	57	WTSWA Fall	15	0	0.95	**	**	-	-	-	-	-	0.24	0.03
Spring														
M	57	WTSEP Fall	23	0.01	1	0.25	0.37	0.03	1	0.96	0.16	61.7	0.09	0.11
Spring														
WTSEP Fall	23	WTSWA Fall	15	0.01	*	0.52	0.91	0.04	0.97	**	*	80.8	0.08	0
WTSEP Spring	23	M	57	0.09	1	*	**	0.11	1	0.15	**	71.4	0.07	0.09
		Spring												
WTSWA Spring	14	M	57	0.02	1	*	0.90	-	-	-	-	-	0.32	0
		Spring												
WTSEP Fall	23	M	12	0.04	1	**	0.89	0.00	0.32	0.70	0.08	62.2	0.08	0
		Fall												
WTSWA Fall	15	M	12	0.01	0.98	*	0.97	-	-	-	-	-	0.08	0
		Fall												

distinct number of occurrences between spring/summer and autumn/winter, supporting previous references to this species as sub-Antarctic (Kullenberg, 1963). Interestingly, our full range calibration ENMs not only reflect the reported north/south seasonal movements of the species, but also the seasonality of the migration between Argentina (spring) and the Malvinas/Falkland Islands (summer). More importantly, all our models for the first modelling approach support the species might be resident in Peru, contradicting current literature (Gochfeld et al., 2020).

During the fall, the South American Tern mostly establishes reproductive colonies along the coasts of Peru, within the Warm Temperate Southeastern Pacific Province, and Brazil, within the Warm Temperate Southwestern Atlantic Province; and in the Magellanic Province during spring (Carlos, 2009; Gochfeld et al., 2020; Portflitt-Toro et al., 2018). This would suggest that the provinces could be delimiting environmentally different conditions for the South American Tern. However, most of our models predicted higher occurrence probability outside the expected areas, supporting that this second approach has limited utility in identifying relevant ecological barriers at least for this seabird. Therefore, our discussion on the species ecological requirements is based on the ENMs obtained from the full-range calibration area.

Differences in the response curves obtained per environmental variable seem to point to interesting environmental differences between seasons. Chlorophyll-a concentration response curves indicate a positive correlation with the occurrence probability of the species during all seasons. Chlorophyll-a has also been often observed as a relevant variable for Procellariiformes from the Southern Atlantic Ocean, as the Grey-Headed Albatross *Thalassarche chrysostoma* (Scales et al., 2016); and other Charadriiformes from the North Pacific Ocean, as the Kelp Gull *Larus dominicanus*, Franklin's Gull *Larus pipixcan* and Grey Gull *Larus modestus* (Weichler et al., 2004). In fact, chlorophyll-a has been used as a proxy of marine productivity and prey availability for several taxa, including seabirds (Friedlaender et al., 2011; Ingenloff, 2017; Tobeña et al., 2016). Chlorophyll-a is an indirect estimator of the biomass of phytoplankton and photosynthetic rate of the primary marine producers (Hu et al., 2012; Sardiña, 2005; Turner, 2004; Yentsch, 1960). This fuels zooplankton and fish production, which ultimately supports higher trophic levels, including large populations of seabirds (Thiel et al., 2007; Weichler et al., 2004). The South American Tern seems so not to be an exception, as fish comprise most of its diet (Alfaro et al., 2011). The species has a generalist feeding strategy, characterized by a broad

dietary niche width (Alfaro et al., 2011; Amundsen et al., 1996). A variety of fish species are part of the diet of this tern in the Atlantic coast, as the pelagic *Engraulis anchoita*, *Anchoa mitchilli*, *Lycengraulis grossidens*, and *Odontesthes argentinensis* (Ajó et al., 2011; Alfaro et al., 2011; Favero et al., 2000; Fracasso et al., 2011). Terns are surface feeding species that make shallow dives into the ocean water (Vandendriessche et al., 2007). Notwithstanding, some demersal fish species are also part of the South American Tern diet (e.g., Bigtooth corvina *Isopisthus parvipinnis*, Striped weakfish *Cynoscion guatucupa*, Argentine croaker *Umbrina canosai*, Silverside *Odontesthes incisa*, King weakfish *Macrodon ancylodon*, Whitemouth croaker *Micropogonias furnieri*, Largehead hairtail *Trichiurus lepturus*, and False hering *Harengula clupeiola*; Ajó et al., 2011; Alfaro et al., 2011; Favero et al., 2000; Fracasso et al., 2011). These demersal fish species can only be obtained through discarded bycatch fish and not by direct capture at deep sea, as observed for other tern species, such as the Royal Tern *Thalasseus maximus* (Bugoni and Vooren, 2005) and the Common Tern *Sterna hirundo* during the non-breeding periods (Bugoni and Vooren, 2004). Commercial fishery is increasing the diversity of fish species present in seabirds' diet, altering their feeding and migratory habits (Favero et al., 2000; Fracasso et al., 2011; Friedlaender et al., 2011; Karpouzi et al., 2007; Weichler et al., 2004). Furthermore, maximum fishing effort occurs during spring and summer along the southern coast of South America, and in the Atlantic coast during winter (Guiet et al., 2019), coinciding with the species migratory behaviour. Additionally, the South American Tern can occasionally exploit other resources. Although fish comprise the larger proportion (82–88%) of the species diet the rest of the year, in the winter season, when fish stocks are limited, crustaceans and insects can also be part of the diet of the South American Tern (Ajó et al., 2011; Alfaro et al., 2011; Fracasso et al., 2011). Therefore, although chlorophyll-a and so marine productivity and prey availability are relevant for the presence of the South American Tern, the species' generalist and opportunistic feeding behaviour might also be contributing for the absence of environmental variation in our models. Despite there are no studies based on the diet of the South American Tern in the Pacific coast, the pelagic Anchoveta *Engraulis ringens* might be an important food resource in that region, as this is the major prey species for the Arctic Tern *Sterna paradisaea* in the Humboldt upwelling at the North Pacific Ocean (Duffy et al., 2013).

For the first modelling approach, the response curves for the sea surface temperature indicate a negative correlation with the occurrence

probability of the species, but only during the spring and summer. Variation in seabird distribution patterns has for long known to be influenced by variation in the sea surface temperature (Gall et al., 2017; Weichler et al., 2004), and the species has been associated to cold fronts before (Kullenberg, 1963). Furthermore, this variable is of great importance in marine ecosystem regulation and its increase leads to algal blooms, which might be beneficial, supporting marine productivity; but also harmful leading to the eutrophication of the ocean (Rivas, 2010; Zohdi and Abbaspour, 2019). Due to climate change, natural but toxic algal blooms are more frequent, associated with a rise on the sea surface temperature since the 1990's (IPCC, 2019; Trainer et al., 2020; Zohdi and Abbaspour, 2019). Seasonal blooms in the Patagonian continental shelf take place during the austral spring and summer, caused by the influence of thermal fronts, i.e., sudden increases in the sea surface temperature that are in general more numerous and intense during these seasons (Poulton et al., 2013; Rivas, 2006; Zohdi and Abbaspour, 2019). This can explain the sea surface temperature seasonal negative effect on the South American Tern occurrence.

Particulate inorganic carbon also presented a negative correlation with the occurrence probability for the South American Tern during fall and winter. Particulate inorganic carbon is one of the principal products of the oceanic photosynthetic activity of phytoplankton (Hopkins et al., 2019). Southern Hemisphere plays a significant role in the temporal and spatial variability in the oceanic particulate inorganic carbon, with highest values observed at the beginning of the austral summer and lowest at the beginning of the austral winter, predominantly off the coasts of Chile and Namibia (Hopkins et al., 2019). During winter and early spring, primary production rates and phytoplankton biomass increase in the southeastern Brazilian coast, related to the nutrients supplied from seasonal displacement of the subtropical convergence and the freshwater discharge of the La Plata River and Patos Lagoon estuary (Ciotti et al., 1995; Lima et al., 1996). The cold, low-salinity sub-Antarctic waters from the Argentinean shelf arriving the southeastern Brazilian coast increases the biological productivity and the dynamics of shelf-sea ecosystem (Lima et al., 1996), which might explain the response of the particulate inorganic carbon to the ENM models in winter.

#### 4.2. Environmental space comparisons for the South American Tern

Most of our results from the 'humboldt' analyses for the equivalence and background statistic suggest that there is limited support for seasonal niche differentiation and divergence along the South American Tern migration route, despite the low values of Schoener's D niche similarity index in our comparisons ( $D \leq 0.19$ ). Similar results for this index were shown by Ponti et al. (2020) for other Charadriiformes species ( $D < 0.1$ ), supporting this might be a general pattern for these birds. However, this interpretation must be done with caution, since Humboldt's niche comparisons might be less efficient when the environmental spaces compared are very similar, but also for taxa with narrow and restricted ranges, due to the inherent limited environmental space available for comparison (Brown and Carnaval, 2019), as verified in our case study.

Some migratory seabird species present a high level of migratory connectivity as well, i.e., most individuals from one breeding population move to the same non-breeding location to form a non-breeding population, with a relatively small proportion of individuals migrating to other wintering areas (Webster et al., 2002). For instance, some tern species with a long-distance migration, such as the Arctic Tern, encompass coastal, oceanic and polar regions (Duffy et al., 2013; Fijn et al., 2013; Redfern and Bevan, 2020); and the Common Tern and the Sandwich Tern *Thalasseus sandvicensis* perform overland migrations across the Teesmouth National Nature Reserve in northeastern England (Ward, 2000). The South American Tern is known to migrate across the Atlantic coast, from the south of Argentina to Brazil and Malvinas/Falkland Islands, and along the Pacific coast from Ecuador to Chile (Gochfeld

et al., 2020). This migratory strategy of the South American Tern might allow the species to maintain similar environmental spaces throughout the year, as supported in our analyses.

Yet, niche overlap tests suggest that South American Tern might occupy different environmental spaces during breeding seasons, particularly during the fall in the Warm Temperate Southeastern Pacific and Warm Temperate Southwestern Atlantic Provinces. This probably results from differences in the choice of microhabitats and reproductive areas that might lead to environmental space differentiation in seabird species (Burg and Croxall, 2001). As the geographic distance between the ranges of two populations increases, shared biotic factors are expected to decrease, and might play different roles in the distribution of the populations (Brown and Carnaval, 2019). Furthermore, the seasonal and spatial differences in microhabitat choices are suspected to play an important role in niche segregation, while avoiding competition amongst tern species (Bugoni and Vooren, 2005).

Last, environmental seasonal comparisons considering the entire species distribution range resulted in a low niche truncation risk, indicating that the measured occupied niche reflects the species' fundamental niche (Brown and Carnaval, 2019). Conversely, environmental comparisons between provinces resulted in a moderated to high niche truncation risk, indicating that the environmental space of each province represents only a sub-portion of the species fundamental niche. This is also consistent with the spurious occurrence probability areas obtained in ENM models by province. Provinces seem to be incomplete representations of the fundamental niche, as their use as calibration areas result in overfitted models (Peterson et al., 2011).

#### 5. Conclusions

Our results refuted our hypothesis that coastal provinces might correspond to environmental variation delimiting distinct ecological niches for seabirds. However, the use of such partitioning allows the detection of regional environmental variation that would be otherwise unnoticed. Furthermore, our regional per season partitioning confirms that, in the ENM procedure for migratory species, either seabirds or other, it is essential to account for the non-equilibrium state of their distributions, and seasonal partitioning of the data is valuable to understand the species dynamics, although such approach has still been seldom used (Ingenloff, 2017). Therefore, we recommend partitioning the occurrence datasets into seasons for ENM of migratory species. Niche truncation analysis seems to be an interesting method to confirm the adequacy of such division. Nonetheless, ecological niche comparisons remain challenging, rendering ambiguous results for seabirds, hindered by the narrow distribution ranges of these species (Brown and Carnaval, 2019).

The potential ecological niche of the South American Tern is driven principally by environmental variables indicative of marine ecosystem regulation, marine productivity, and prey availability, as observed for other seabirds (Gall et al., 2017; Rivas, 2010; Scales et al., 2016; Thiel et al., 2007; Weichler et al., 2004). The temporal variability we observe in the potential niche of the South American Tern does not seem to be enough to cause environmental divergence and differentiation. Nonetheless, we highlight that investigation on the role of fisheries bycatch as food resource and driver of niche divergence is still lacking, for this and other seabirds, particularly in the Pacific coast. Importantly, the influence of sea surface temperature (and sea surface temperature increase; IPCC, 2019) is not homogeneous throughout the South American coasts per season. How this variation will impact population persistence and connectivity between populations of the South American Tern and other seabirds is unclear, since genetic population structure and demographic trends on this and other species are poorly known (Faria et al., 2010; Gochfeld et al., 2020). Importantly, the year-round high occurrence probability area in coastal Peru that we have identified in our models, corresponding to the northernmost portion of the species distribution and potentially seasonally isolated, points to a probable population



structure, which should be further investigated. Moreover, given that more than 20% of the recently globally assessed seabird species are estimated to be negatively impacted by climate change alone (Dias et al., 2019), we emphasize a thorough assessment of the demographic trends and population structure for the South American Tern are urgently needed.

## Funding

**Roxiris A. Azuaje-Rodríguez** received a PhD scholarship from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Brazil. **Sofia Marques Silva** was supported by European Regional Development Fund through COMPETE program and by Fundação para a Ciência e Tecnologia, Portugal (PTDC/BIA-MIC/27,995/2017; POCI-01-0145-FEDER-027,995). **Caio J. Carlos** was supported by a fellowship from the Programa Nacional de Pós-Doutorado/Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (PNPD-CAPES), Brazil.

## CRediT authorship contribution statement

**Roxiris A. Azuaje-Rodríguez:** Methodology, Software, Validation, Data curation, Writing – original draft. **Sofia Marques Silva:** Writing – review & editing, Supervision, Visualization. **Caio J. Carlos:** Writing – review & editing, Visualization, Supervision.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgements

We thank K. Bohrer do Amaral, E. Ilha, B. Naimi, J.L. Brown, B. Muscarella, J. Kass, G. Ribeiro, B. Simons, C. Xavier, O. Aldana, A. Penagos, J. Rosoni, H. Krammes, A. Carneiro, D. Janish and F. Tirelli for technical support and constructive comments to this research. We also acknowledge the comments of suggestions of two anonymous reviewers that helped to improve the quality of this manuscript.

## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2021.109804.

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