



UFRGS
UNIVERSIDADE FEDERAL
DO RIO GRANDE DO SUL



**INSTITUTO DE BIOCÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA ANIMAL**

ROXIRIS AUXILIADORA AZUAJE RODRÍGUEZ

**ESTRUTURA POPULACIONAL DE *Sterna hirundinacea* Lesson, 1831 (Aves:
CHARADRIIFORMES) E AS IMPLICAÇÕES PARA SUA CONSERVAÇÃO**

PORTO ALEGRE

2022

ROXIRIS AUXILIADORA AZUAJE RODRÍGUEZ

ESTRUTURA POPULACIONAL DE *Sterna hirundinacea* Lesson, 1831 (Aves: CHARADRIIFORMES) E AS IMPLICAÇÕES PARA SUA CONSERVAÇÃO

Tese apresentada ao Programa de Pós-Graduação em Biologia Animal, Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como requisito parcial à obtenção do título de Doutora em Biologia Animal.

Área de concentração: Biologia comparada

Orientador: Dr. Caio José Carlos

Coorientadora: Dra. Sofia Marques Silva

PORTO ALEGRE

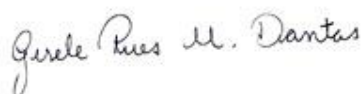
2022

ROXIRIS AUXILIADORA AZUAJE RODRÍGUEZ

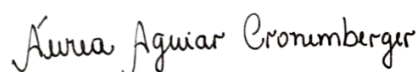
ESTRUTURA POPULACIONAL DE *Sterna hirundinacea* Lesson, 1831 (Aves: CHARADRIIFORMES) E AS IMPLICAÇÕES PARA SUA CONSERVAÇÃO

Aprovada em 13 de outubro de 2022.

BANCA EXAMINADORA



Dra. Gisele Pires de Mendonça Dantas
Pontifícia Universidade Católica de Minas Gerais - PUC Minas



Dra. Aurea Aguiar Cronemberger
Universidade Federal do Piauí – UFPI



Dr. Ismael Franz
Universidade Federal do Rio Grande do Sul - UFRGS

APRESENTAÇÃO

Esta tese de doutorado é apresentada conforme Resolução N° 38/2019, deste Programa de Pós-Graduação em Biologia Animal (PPG-BAN) da Universidade Federal do Rio Grande do Sul, que institui procedimentos e normas para apresentação e avaliação da Dissertação de Mestrado e da Tese de Doutorado. O texto principal desta tese está estruturado sob a forma de dois artigos científicos, redigidos em língua inglesa, o primeiro deles já publicado na revista *Ecological Modelling* (Qualis A1) e o segundo visando à submissão na revista *Marine Biology, International Journal on Life in Oceans and Coastal Waters* (Qualis A1). Este trabalho está de acordo com as “normas aos autores” dos referidos periódicos, disponíveis nos seguintes links: *Ecological Modelling* – <https://www.elsevier.com/journals/ecological-modelling/0304-3800/guide-for-authors>, *Marine Biology* – <https://www.springer.com/journal/227/submission-guidelines>. De acordo com o Artigo 43° do Regimento do PPG-BAN, os artigos, que compõe a parte central desta tese, estão acompanhados de dois capítulos extras. O primeiro, a introdução geral, contém uma revisão sobre o problema abordado pelo trabalho, e traz as hipóteses, os objetivos e uma síntese dos resultados gerais do trabalho. O segundo, apresenta as principais conclusões. Ambos os capítulos introdutório e conclusivo estão redigidos em língua portuguesa. Adicionalmente, de acordo com a Resolução N° 40/2021 do mesmo PPG-BAN, é listado abaixo o documento referente ao Cadastro junto ao Sistema de Gestão do Patrimônio Genético (SISGEN); e, para além disso, também são listadas as autorizações de importação/exportação das amostras de tecido provenientes das coleções e museus que contribuiram com este projeto e uma declaração informando que não houve coleta de material neste projeto, mas todas as amostras foram cedidas por outras instituições/projetos de pesquisa; por isso, não houve necessidade de obtenção de aprovação por CEUA.

CIP - Catalogação na Publicação

Azuaje Rodríguez, Roxiris Auxiliadora
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Orientador: Caio José Carlos.

Coorientador: Sofia Marques Silva.

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2022.

1. Alocronia. 2. estrutura genética. 3. morfologia.
4. modelagem de nicho ecológico. 5. provincias
costeiras. I. Carlos, Caio José, orient. II. Marques
Silva, Sofia, coorient. III. Título.

1. Comprovante de cadastro no Sistema nacional de gestão do patrimônio genético e do conhecimento tradicional associado (SISGEN).



Ministério do Meio Ambiente
CONSELHO DE GESTÃO DO PATRIMÔNIO GENÉTICO
SISTEMA NACIONAL DE GESTÃO DO PATRIMÔNIO GENÉTICO E DO CONHECIMENTO TRADICIONAL ASSOCIADO

Comprovante de Cadastro de Acesso
Cadastro nº ABA1276

A atividade de acesso ao Patrimônio Genético, nos termos abaixo resumida, foi cadastrada no SisGen, em atendimento ao previsto na Lei nº 13.123/2015 e seus regulamentos.

Número do cadastro: **ABA1276**
Usuário: **Caio José Carlos**
CPF/CNPJ: **027.076.284-17**
Objeto do Acesso: **Patrimônio Genético**
Finalidade do Acesso: **Pesquisa**

Espécie

Sterna hirundinacea

Título da Atividade: **Estrutura populacional de Sterna hirundinacea Lesson, 1831 (Aves: Charadriiformes) e as implicações para a conservação**

Equipe

Caio José Carlos	UFRGS
Roxiris Auxiliadora Azuaje Rodríguez	UFRGS

Data do Cadastro: **25/10/2018 18:21:04**
Situação do Cadastro: **Concluído**

Conselho de Gestão do Patrimônio Genético
Situação cadastral conforme consulta ao SisGen em 15:17 de 13/09/2022.



SISTEMA NACIONAL DE GESTÃO
DO PATRIMÔNIO GENÉTICO
E DO CONHECIMENTO TRADICIONAL
ASSOCIADO - **SISGEN**



Ministério do Meio Ambiente
CONSELHO DE GESTÃO DO PATRIMÔNIO GENÉTICO

SISTEMA NACIONAL DE GESTÃO DO PATRIMÔNIO GENÉTICO E DO CONHECIMENTO TRADICIONAL ASSOCIADO

Certidão
Cadastro nº ABA1276

Declaramos, nos termos do art. 41 do Decreto nº 8.772/2016, que o cadastro de acesso ao patrimônio genético ou conhecimento tradicional associado, abaixo identificado e resumido, no Sistema Nacional de Gestão do Patrimônio Genético e do Conhecimento Tradicional Associado foi submetido ao procedimento administrativo de verificação e não foi objeto de requerimentos admitidos de verificação de indícios de irregularidades ou, caso tenha sido, o requerimento de verificação não foi acatado pelo CGen.

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SISTEMA NACIONAL DE GESTÃO
 DO PATRIMÔNIO GENÉTICO
 E DO CONHECIMENTO TRADICIONAL
 ASSOCIADO - **SISGEN**

2. Carta de empréstimo de amostras pela University of Kansas, Natural History Museum.



Natural History Museum

15 March 2019

To Whom It May Concern:

This letter is to serve as a declaration that we will send Roxiris Azuaje Rodriguez at the Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil scientific tissue samples listed below. The tissue samples, ca. 2 x 2 mm, will be sent in 100 % ethanol. All of the samples are from *Sterna hirundinacea* (family Laridae) that were collected in Argentina and Chile from 1985 and 1987.

Sterna hirundinacea:



10 samples from Argentina
7 samples from Chile

Sincerely,

A handwritten signature in blue ink that reads 'Mark Robbins'.

Mark Robbins
Ornithology Collection Manager

3. Licença de exportação para a University of Kansas, Natural History Museum emitida pelo Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA).

 REPÚBLICA FEDERATIVA DO BRASIL MINISTÉRIO DO MEIO AMBIENTE - MMA INSTITUTO BRASILEIRO DO MEIO AMBIENTE E DOS RECURSOS NATURAIS RENOVÁVEIS - IBAMA SCEN Trecho 2 - Ed. Sede - Caixa Postal nº 09870 - CEP 70818-900 - Brasília-DF		 INSTITUTO BRASILEIRO DO MEIO AMBIENTE E DOS RECURSOS NATURAIS RENOVÁVEIS - IBAMA		1) Pag. Nº 1/1
				2) Data Emissão/Issuing Date: 06/04/2019
				3) Válido Até/Valid Until: 06/10/2019
4) Licença nº/Permit n°: 19BR031250/DF		6) Selo nº/Stamp n°: ***** 7) Selo/Stamp *****		8) Controle/Check ¹: PTYATR42IUSEIB7K 9) Autoridade Adm. Emitente/Issuing Management Authority <i>Claudia M. C. de Mello</i> Assinatura/Signature
5) Licença de/Permit for Importação/Import				<i>Claudia Maria C. Mello</i> Management authority CITEA / BRAZIL
10) Importador/Importer ROXIRIS AUXILIADORA AZUAJE RODRIGUEZ AVENIDA GOETHE 57 PORTO ALEGRE - 90430100 fone: 51981006103 - roxiris6@gmail.com Brasil - BR		11) Exportador(Re-exportador)/Exporter(Re-exporter) Mark B. Robbins 1345 Jayhawk Blvd. Lawrence, Kansas Lawrence, Kansas - 66045 fone: - Estados Unidos da América - US		
12) País Importador/Country of Import Brasil - BR		13) País Exportador(Re-exportador)/Country of Export(Re-export) Estados Unidos da América - US		
14) Objetivo da Operação/Purpose of the transaction S - Scientific/Fins científicos...				
15) Condições Especiais/Special Conditions For live animals, this permit or certificate is only valid if the transport conditions conform to the Guidelines for Transport and preparation for shipment of live wild animals and plants or, in the case of air transport, to the IATA Live Animals Regulations				
16) Dados do Transporte/Transportation Data Local/Place: ALF/Al Porto Alegre Data Provável/Probable Date: 08/05/2019 ESTA LICENÇA É VÁLIDA SOMENTE PARA UMA OPERAÇÃO/ THIS PERMIT OR CERTIFICATE IS ONLY VALID FOR ONE SHIPMENT.				
17) Item		18) Produto/Product		19) Quantidade-Unidade Medida/Quantity Unit
20) Espécie: nome científico nome vulgar/ Species: scientific name common name		21) Anexo/Origem Appendix/Source		23) Cód. País de Origem-Comprovante-Data Country of Origin-Permit-Date 24) Cód. País de reexportador-Certificado-Data Country reexportation-Certificate-Date
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				19) -- 17,00 UN -- 23) - - 24) - -
----- Fim dos Itens/Itens End -----				
<p>"Esta licença não autoriza o uso do material biológico para acessar informações de origem genética, contida no todo ou em parte de espécime vegetal, fungo, microbiano ou animal; em substâncias provenientes do metabolismo desses seres vivos e de extratos obtidos desses organismos vivos ou mortos, encontrados em condições /in situ/, inclusive domesticada, ou mantidos em coleções /ex situ/, desde que coletados em condições /in situ/, no território nacional, na plataforma continental ou na zona econômica exclusiva, visando atividade exploratória para identificar componentes do patrimônio genético e informação sobre o conhecimento tradicional associado, com potencial de uso comercial"</p> <p>"This permit does not extend to the use of biological material to access genetic information, contained in the whole or parts of plants, fungus, microorganisms or animals specimens; in substances derived from the metabolism of these living beings or from extracts obtained from live or dead specimens, occurring in situ conditions, including domestic ones, or kept in ex situ collections, if obtained in situ conditions, in national territory, the continental shelf or the exclusive economic zone, aiming at prospecting for identification of components of the genetic patrimony and/or information about associated traditional knowledge e with potential commercial use."</p>				
25) Endosso da Aduana/Customs Endorsement				
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ASSINAT/SIGNATURE _____				
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4. Licença de importação emitada pelo Falkland Islands Government slands



The Falkland Islands Government

Secretariat Stanley Falkland Islands
 Telephone: (500) 28427
 E-mail: environmental.officer@sec.gov.fk

Research Licence No: R13/2021

CONSERVATION OF WILDLIFE AND NATURE ORDINANCE 1999

SECTION 9

LICENCE TO CARRY OUT SCIENTIFIC RESEARCH

1. Licensee:

Name of the person leading the research	Roxiris A. Azuaje Rodríguez
Affiliation	Instituto de Biociências – Departamento de Zoologia Universidade Federal do Rio Grande do Sul
Position	PhD student
Postal Address	Laboratório de Sistemática e Ecologia de Aves e Mamíferos Marinhos (LABSMAR) Instituto de Biociências – Departamento de Zoologia Universidade Federal do Rio Grande do Sul Porto Alegre, RS, Brasil.
Phone number	Cel.: +55 (51)981006103
Email	roxiris6@gmail.com

2. Nature of licence:

2.1. This licence is issued to Roxiris A. Azuaje Rodríguez under Section 9 of the Conservation of Wildlife and Nature Ordinance 1999. It is granted to Roxiris A. Azuaje Rodríguez to permit their staff and bona fide field assistants or researchers employed on their behalf or under their overall jurisdiction. It is granted only for the following activities using methods specified in the research licence application of "Population structure of the South American Tern, *Sterna hirundinacea* (Aves: Charadriiformes) and conservation implications" submitted to the Environmental Officer on the 18th August 2021:

Sampling

We will use tissues, blood or feathers samples of *Sterna hirundinacea* specimens from colonies distributed on the Atlantic and Pacific coasts of South America and the Falkland Islands. Some tissue (23) and blood (15) samples will be provided by Ornithological museums and institutions

(Museu de Ciências Naturais da UFRGS (MUCIN) – Brasil, Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (MCP) – Brasil, Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN) – Argentina, Natural History Museum, KU Biodiversity Institute at the University of Kansas (UK) – USA, Universidad Científica del Sur. Facultad de Ciencias Ambientales – Perú). Others samples will be collected directly on the reproductive colonies by using less invasive techniques, such as collecting feathers from live captured specimens or whenever is possible tissue from dead specimens founds on beaches. We will receive help in the tissue and feathers samples collection of *Sterna hirundinacea* individuals located at the breeding sites in the Atlantic and Pacific coast from the following organizations and programs: Centre of Coastal, Limnological and Marine Studies (CECLIMAR), UFRGS, Brazil; AVESAMAR, Brazil; Falkland Conservation, Falkland Islands. In particular, will be only use tissue collected from dead specimens founds on Falkland islands beaches.

DNA extraction, amplification and sequencing

Total DNA will be extracted using a phenol-chloroform protocol. Amplification of the cytochrome b mitochondrial DNA (cytb, mtDNA) will be performed using primers L15008 and H15326. Single nucleotide polymorphisms (SNPs) will also be assessed, through genotyping by sequencing (GBS). Part of the laboratory procedures will be carried out in the Laboratory of Extraction and Amplification of DNA of the Department of Zoology / UFRGS/ Brazil. Sequencing will be complete by MACROGEN KOREA and by FLORAGENEX.

Molecular data analyses

Nucleotide sequences obtained will be edited manually using BioEdit software (Hall, 1999) and aligned using the default settings of Clustal W algorithm (Thompson et al., 1994) implemented in BioEdit. DnaSP software will be used to estimate genetic parameters, such as nucleotide and haplotype diversity, neutrality tests (Tajima's D and R2) and recombination tests for the nuclear genes (Hudson & Kaplan 1985, Hudson et al. 1987, Rozas et al. 2001, Librado & Rozas 2009). Mega software will be used to estimate genetic distances for mitochondrial genes within and among populations (Kumar et al., 2016) and Haplotype viewer software (Salzburger et al., 2011) to construct haplotype networks. Arlequin software will be used to calculate genetic differentiation indices (Fst) (Excoffier & Lischer, 2010).

For SNPs data, quality control and trimming of reads will be performed in FastQC (Wingett & Andrews, 2018). Genome assemblage will be performed using SAMtools, using chicken (NCBI code GCA_000002315.3) or zebrafish (NCBI code: GCF_000151805.1) reference genomes (Li et al., 2009). Heterozygosity will be assessed using VCFtools (Danecek et al., 2011). The SNP filtering will be done using SNPRelate package in R (Zheng et al., 2012). This filtering includes: removing multi-allelic, monomorphic and low-quality positions; and filter SNPs with a linkage disequilibrium (LD). Initial analysis of population structure will be carried out by principal components analysis (PCA) using the SNPRelate package (Zheng et al., 2012) and plotted using ggplot2 package (Wickham, H. 2016). Further population structure will be estimated in STRUCTURE (Pritchard et al., 2000). TreeMix will be used to estimate events of migration and relation between populations (Pickrell, J. and Pritchard, 2012). These data will support migration rates and divergence time estimates from DIYABC (Cornuet et al., 2008).

2.2. This licence shall not be construed as authorising the licensee to enter upon the land of another without the owner's permission or consent.

2.3. This licence shall not constitute a permit to collect biological samples from protected species of the Conservation of Wildlife and Nature Ordinance 1999 other than those mentioned in 2.1 above.

2.4. This licence does not constitute a permit to remove biological items from protected species from the Falkland Islands. An export licence should be sought from the Customs and Immigration Department to allow for the removal of any biological material or protected species from the Falkland Islands.

3. Period of licence

3.1 This licence is valid for the period commencing on 1st April 2021 and terminating on 31st March 2022.

3.2 This licence may be revoked at any time by the Governor, but otherwise shall be valid for the period stated in paragraph 3.1.

4. Conditions of licence

4.1 This licence is issued on condition that the licensee shall:

- a) Submit to the Environmental Officer, Policy and Economic Development Unit, The Secretariat, Stanley, Falkland Islands, **not later than 30th June 2023, a report of the scientific findings;** and
- b) Deposit with the Environmental Officer copies of all subsequent reports on the research work carried out.
- c) Deposit with the Environmental Officer copies of the metadata for any data collected as part of this study.

5. Purpose of Research



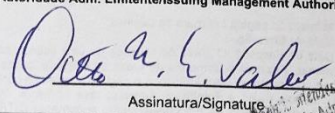
The purpose of the research work carried out by the licensee is set out in the proposal to the Environmental Officer on the 18th August 2021.

Signed:




Caroline McLaren
Assistant Environmental Officer
Dated: 18th August 2021

5. Licença de exportação para Falkland Islands Government emitida pelo Instituto Brasileiro do Meio Ambiente e dos recursos Naturais Renováveis (IBAMA).


 REPÚBLICA FEDERATIVA DO BRASIL MINISTÉRIO DO MEIO AMBIENTE - MMA INSTITUTO BRASILEIRO DO MEIO AMBIENTE E DOS RECURSOS NATURAIS RENOVÁVEIS - IBAMA SCEN Trecho 2 - Ed. Sede - Caixa Postal nº 69870 - CEP 70818-900 - Brasília-DF		 INSTITUTO BRASILEIRO DO MEIO AMBIENTE E DOS RECURSOS NATURAIS RENOVÁVEIS - IBAMA		1) Pag. Nº 1/1 2) Data Emissão/Issuing Date: 25/05/2021 3) Válido Até/Valid Until: 25/11/2021																	
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6. Guia de Remessa de material do Centro de Estudos Costeiros, Limnológicos e Marinhos. Museu de Ciências Naturais (MUCIN).



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UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
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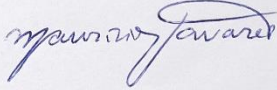
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<input type="checkbox"/> Empréstimo	<input checked="" type="checkbox"/> Envio de amostras
<input type="checkbox"/> Doação para coleção	<input type="checkbox"/> Permuta
<input type="checkbox"/> Outro:	<input type="checkbox"/> Para identificação

Enviamos o material abaixo relacionado:

Código	Espécie	Material enviado
AM 208	<i>Sterna hirundinacea</i>	Alíquota de tecido
AM 234	<i>Sterna hirundinacea</i>	Alíquota de tecido
AM 523	<i>Sterna hirundinacea</i>	Alíquota de tecido
2018	<i>Sterna hirundinacea</i>	Alíquota de tecido
2228	<i>Sterna hirundinacea</i>	Alíquota de tecido
2247	<i>Sterna hirundinacea</i>	Alíquota de tecido
5339	<i>Sterna hirundinacea</i>	Alíquota de tecido
5393	<i>Sterna hirundinacea</i>	Alíquota de tecido
5412	<i>Sterna hirundinacea</i>	Alíquota de tecido


Obs.: Tese de doutorado PPGBAN-UFRGS

Remetente:
Maurício Tavares
MUCIN/UFRGS
CECLIMAR/CLN/UFRGS

Assinatura: 

Local e data: Imbé, 11 de agosto de 2021

Destinatário:
Roxiris A. Azuaje Rodríguez
Porto Alegre
PPGBAN-UFRGS

Assinatura: 

Local e data: Imbé, 11 de agosto de 2021

7. Declaração



Porto Alegre, 30 de novembro de 2022

À Comissão Coordenadora
Programa de Pós-graduação em Biologia Animal (PPGBAN),
UFRGS

Prezados:

Ao cumprimentá-los muito respeitosamente, vimos, por meio desta, declarar que não foram realizadas coletas por este projeto, mas todas as amostras utilizadas foram obtidas por outras instituições/projetos de pesquisa, e.g., o Centro de Estudos Costeiros, Limnológicos e Marinhos. Museu de Ciências Naturais (MUCIN), University of Kansas - Natural History Museum e Falkland Conservation, Projeto de Pesquisa e Conservação de Aves Marinhas e Ambientes Insulares do Litoral de SP - AVESAMAR, e cedidas para as análises aqui realizadas. Por esse motivo, não foi necessária a obtenção de aprovação pelo CEUA.

Sem mais para o momento, estamos à disposição para eventuais esclarecimentos adicionais necessários.

Atenciosamente,

Roxiris A. Azuaje Rodríguez
Discente

Caio José Caio
Orientador

AGRADECIMENTOS

Escrevi esta tese graças a ajuda de muitas pessoas e apoio de diversas entidades.

Por isso agradeço ao Programa de Pós-Graduação em Biologia Animal da Universidade Federal do Rio Grande do Sul, pela oportunidade de frequentar esse curso de doutorado.

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SUMÁRIO

RESUMO.....	19
ABSTRACT.....	20
INTRODUÇÃO GERAL.....	22
REFERÊNCIAS BIBLIOGRÁFICAS.....	31
CAPÍTULO 1.....	37
Abstract.....	37
Introduction.....	38
Material and Methods.....	41
Results.....	45
Discussion.....	46
Conclusion.....	51
Funding.....	52
Credit authorship contribution statement.....	52
Declaration of Competing Interest.....	52
Acknowledgements.....	53
References.....	53
Supplementary Material.....	67
CAPÍTULO 2.....	114
Abstract.....	114
Introduction.....	115
Material and Methods.....	118
Results.....	122
Discussion.....	124
Conclusion.....	128
Acknowledgements.....	129
Author contributions.....	129
Funding.....	130
Data availability.....	130
Declarations.....	130
References.....	131
Supplementary Material.....	149
CONCLUSÕES GERAIS.....	169
REFERÊNCIAS BIBLIOGRÁFICAS.....	171
ANEXO	173

RESUMO

O trinta-réis-de-bico-vermelho *Sterna hirundinacea* é uma ave marinha migratória pouco conhecida. A espécie está distribuída na maioria das províncias costeiras da América do Sul, ao longo dos oceanos Pacífico e Atlântico, incluindo as Ilhas Malvinas/Falkland. Apesar de estar globalmente não ameaçada em escala local, as populações da espécie são afetadas pela perturbação humana em áreas de nidificação. A época de reprodução da espécie varia com a latitude e estação do ano, ocorrendo durante a primavera no Sul e durante o outono no norte das áreas de ocorrência da espécie. Estas observações apontam para populações eventualmente estruturadas e distintas ao longo da distribuição da espécie, e que parecem ser coincidentes com as províncias marinho costeiras. No entanto, a hipótese de estruturação ecológica do trinta-réis-de-bico-vermelho nunca foi testada. Assim, no primeiro capítulo, testou-se a diferenciação do espaço ambiental no nicho ecológico da espécie, usando diferentes províncias marinho costeiras e ao longo de toda a área de distribuição da espécie. Os modelos de nicho ecológico foram realizados para estação do ano, para cada uma das províncias costeiras durante os períodos reprodutivos. No segundo capítulo avaliamos a variação morfológica e genética do trinta-réis-de-bico-vermelho ao longo de sua área de distribuição, ampliando os dados morfológicos e moleculares disponíveis até o momento. Também descrevemos a história demográfica e o tempo de diversificação da espécie usando linhagens matrilineares. Não encontramos nichos ecológicos diferentes ao longo do ano, exceto durante a época de reprodução, particularmente entre as províncias do Sudoeste Temperado Quente do Atlântico e Sudoeste Temperado Quente do Pacífico no outono. Os resultados obtidos apontam que o comportamento migratório da espécie e a seleção de diferentes micro habitats e áreas reprodutivas possam estar influenciando o espaço ambiental de *Sterna hirundinacea*. Além disso, não encontramos estruturação morfológica ou genética entre as populações da espécie. Em vez disso, os dados recolhidos indicaram somente algumas diferenças geográficas na largura do bico, comprimento do tarso e total da cauda para os espécimes da província Sudoeste Temperado Quente do Pacífico e a presença de fluxo gênico entre todas as populações amostradas. Pode-se notar porém, que nossos dados revelam a existência de dimorfismo sexual para a espécie. Assim, parece que as diferenças ambientais de cada província marinho costeira e a alocria nas populações costeiras do Sul e do Norte não estão causando diferenciação genética e isolamento entre as

populações de trinta-réis-de-bico-vermelho. Sua forte conectividade migratória, acompanhada pelo comportamento não filopátrico, estará contribuindo para a manutenção do fluxo gênico entre as populações do trinta-réis-de-bico-vermelho.

Palavras chave: Alocronia, estrutura genética, morfologia, modelagem de nicho ecológico, províncias costeiras.

ABSTRACT

The South American tern *Sterna hirundinacea* is a poorly known migratory seabird. The species is distributed in most of the coastal provinces of South America, along the oceans Pacific and Atlantic, including the Malvinas/Falkland Islands. Despite being globally unthreatened, on a local scale, populations of the species are affected by human disturbance at nesting sites. The species' breeding season varies with latitude and season, occurring during spring in the south and fall in the north of the areas where the species occurs. These observations point to populations that are eventually structured and distinct along the species' distribution, which appears to be coincident with the coastal marine provinces. However, the South American Tern's ecological structuring hypothesis has never been tested. Thus, in the first chapter, we tested the differentiation of the environmental space in the species' ecological niche, using different marine coastal provinces and along the species' entire distribution area. The ecological niche models were performed for each season of the year and coastal provinces during the reproductive periods. Furthermore, in the second chapter, we evaluated the morphological and genetic variation of the South American Tern throughout its distribution area, expanding the morphological and molecular data available so far. In addition, using matrilineal lineages, we described the demographic history and species diversification time. We did not find 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. The results indicate that the species' migratory behavior and the selection of different microhabitats and reproductive areas may influence its environmental space. Furthermore, we did not find morphological or genetic structuring among populations of the South American tern. Instead, the data collected indicated only some geographic differences in the width of the bill, length of tarsus and

total tail for specimens from the Warm Temperate Southeastern Pacific and the presence of gene flow among all populations sampled. It should be noted, however, that our data reveal the existence of sexual dimorphism for the species. Thus, it appears that the environmental differences of each marine coastal province and the allochronic isolation of the southern and northern populations are not causing genetic differentiation and isolation between the South American tern populations. The strong migratory connectivity, accompanied by non-philopatric behavior, will contribute to the maintenance of gene flow between the South American Tern populations.

Keywords: Allochrony, coastal provinces, ecological niche modeling, genetic structure, morphology.

INTRODUÇÃO GERAL

1. Taxonomia integrativa, diversidade biológica e conservação

A taxonomia integrativa é uma abordagem que procura a congruência entre várias linhas de evidência, como distintos caracteres (por exemplo, genéticos, morfológicos, comportamentais e ecológicos), assim como também distintas metodologias (tais como, filogenia e modelagem de nicho ecológico) para a delimitação das espécies (DAYRAT, 2005; DE QUEIROZ, 2007; SCHLICK-STEINER, 2010; CARTSTENS *et al.*, 2013; PANTE *et al.*, 2015). Sua aplicação é recomendável já que, em princípio, permite uma delimitação mais rigorosa e confiável das espécies naturais, além de auxiliar na detecção de espécies ditas crípticas, i.e., duas ou mais espécies distintas que são erroneamente classificadas sob o nome de uma só espécie e que são consideradas morfológicamente indistinguíveis (BICKFORD *et al.*, 2007). Assim, o recurso a estudos integrativos contribui para estimativas mais acuradas da biodiversidade (DAYRAT, 2005; SCHLICK-STEINER, 2010). Adicionalmente, uma correta delimitação de espécies ajuda a distinguir aquelas globalmente ameaçadas de extinção das sujeitas somente a ameaças locais ou até mesmo não ameaçadas. A obtenção de informações apropriadas com respeito à biologia evolutiva, filogeografia, ecologia das espécies e suas populações locais promove estratégias mais efetivas e adequadas para a conservação biológica (MACE, 2004; FRANKHAM *et al.*, 2008).

A diversidade genética é definida como a variedade de alelos e genótipos diferentes presentes entre as espécies ou populações (FRANKHAM *et al.*, 2008). Essa diversidade pode ou não ser manifestada na forma de diferenças fisiológicas, morfológicas, comportamentais, entre outras (i.e., diferentes fenótipos); e, quanto maior a diversidade genética de uma espécie, maior é a probabilidade de existirem fenótipos distintos. Assim, a diversidade genética é necessária para que as populações se adaptem às mudanças ambientais, fornecendo informações herdáveis para a manifestação de fenótipos que favorecem a manutenção das espécies face às novas condições. Por isso, a manutenção da diversidade genética é importante para a prevalência das espécies (HEYWOOD; WATSON, 1995; FRANKHAM *et al.*, 2008). A diversidade genética pode estar igualmente distribuída ao longo da área de ocorrência de uma espécie ou não. A estruturação genética corresponde a diferenças significativas nas frequências alélicas (ou de alelos, i.e., cada uma das formas ou sequência de nucleótideos existentes para um gene)

nas populações, havendo coerência geográfica na distribuição desses alelos pela população. Assim, a estruturação genética populacional é identificada por meio do mapeamento dos diferentes alelos sobre as localidades geográficas ao longo da área de ocorrência da espécie em análise (FRANKHAM *et al.*, 2008). Conhecer a diversidade e estruturação genéticas das populações dentro de uma espécie é importante para a compreensão dos processos responsáveis por sua diferenciação (i.e., formação de populações geneticamente distintas) e até mesmo pela origem da diversidade biológica e especiação, ou surgimento de novas espécies (FRIESEN *et al.*, 2007a; FRANKHAM *et al.*, 2008). Esse conhecimento permite identificar Unidades Evolutivas Significativas (UESs), ou populações diferenciadas geneticamente dentro de uma mesma espécie, facilitando, desse modo, o estabelecimento de prioridades para a conservação no caso de *taxa* (nesse caso, espécies ou populações) ameaçados (RYDER, 1986; WAPLES, 1991; MORITZ, 1994; HEY *et al.*, 2003). Existem diversos mecanismos que podem influenciar na estruturação genética e diminuir o fluxo gênico entre as populações naturais. Especificamente (mas não exclusivamente) em aves marinhas (FRIESEN *et al.*, 2007a), esses mecanismos podem ser resultado de barreiras geográficas, históricas ou contemporâneas, que reduzem o contato de populações entre lados opostos da barreira (STEEVES; ANDERSON; FRIESEN, 2005). Adicionalmente, podem ser os fatores climáticos (NUSS *et al.*, 2016), ou ainda, resultado de barreiras não físicas e processos intrínsecos, relacionados ao comportamento, tais como escolha de micro-habitats e áreas (não) reprodutivas (BURG; CROXALL, 2001) ou de parceiros para a reprodução. Mas também a filopatria, ou seja, a tendência de um animal retornar à mesma área de reprodução (MILOT *et al.*, 2008; COULSON, 2016), rotas migratórias (ROLSHAUSEN *et al.*, 2013) e isolamento alocrônico, i.e., separação de populações durante o período reprodutivo (HENDRY; DAY 2005; FRIESEN *et al.*, 2007b).

2. *Morfologia e diversidade biológica*

Estudos morfológicos são também uma importante ferramenta tanto para a identificação bem como para a classificação de espécies de aves. As aves apresentam grande variação morfológica intra e interespecífica, mas também podem apresentar variações individuais como dimorfismo sexual, a variação etária e sazonal (TOPFER, 2018). Esta variação morfológica, além de estar influenciada por fatores genéticos, também pode ser considerada como adaptação funcional a diferentes condições ambientais em distintas

áreas geográficas ou diferentes comportamentos (BULL, 2006; TOPFER, 2018). Por exemplo, populações de uma mesma espécie podem apresentar variação no tamanho do corpo influenciada pelos gradientes ambientais ao longo de sua área geográfica (WOJCZULANIS-JAKUBAS, 2011). Por outro lado, também podem existir diferenças morfológicas entre espécies de aves influenciadas pelo seu tipo de comportamento alimentar e tipo de voo (HERTEL; BALLANCE, 1999). Estas variações geográficas na morfologia podem ser contínuas conhecidas também como variação clinal, ou podem ser descontínuas (TOPFER, 2018). Em particular, existem diversos estudos mostrando uma ampla variação morfológica entre populações de espécies de aves marinhas ao longo da sua área de distribuição (GRANADEIRO, 1993; MOUM; ARNASON, 2001; LIEBERS; HELBIG, 2002; BULL, 2006; LOMBAL *et al.*, 2020; LARANJEIRO *et al.*, 2022). Atualmente existem também uma ampla variedade de métodos para poder avaliar esta variação morfológica presente nas espécies, por exemplo, análises de morfometria linear e geométrica; (WINKER, 1998; ADAMS; ROHLF; SLICE, 2013), métodos estatísticos univariados e multivariados (ZAR, 1999) e análise espectrofotométrica da plumagem (BLEIWEISS, 2005). Com respeito a morfometria linear, as medidas mais comumente utilizadas em estudos de aves incluem o comprimento do bico, asa, cauda e a massa corporal (WINKER, 1998).

3. Modelagem de nicho ecológico em aves marinhas migratórias.

Adicionalmente, existem outras ferramentas que contribuem para o conhecimento da diversidade biológica e na conservação das espécies, como a modelagem de nicho ecológico ou modelagem de nicho. A modelagem de nicho usa as variáveis ambientais e os registros de ocorrência das espécies para estimar sua área de distribuição potencial (PHILLIPS *et al.*, 2006; FRANKLING, 2010), com fim de estimar mudanças nos limites de distribuição de espécies (INGENLOFF *et al.*, 2017; AZUAJE-RODRÍGUEZ *et al.*, 2020; RATHER *et al.*, 2020), auxiliar na proposição de estratégias eficazes para a conservação (DE CARVALHO *et al.*, 2017; DIAS *et al.*, 2017; OPEL *et al.*, 2018; PARREIRA *et al.*, 2019), e comparar nichos ecológicos entre espécies (TOCCHIO *et al.*, 2015). Estas comparações foram realizadas inicialmente no espaço geográfico, avaliando a similaridade de nicho entre espécies que ocorrem na mesma área geográfica (WARREN *et al.*, 2008; WARREN *et al.*, 2010). Atualmente, é possível avaliar a similaridade de nicho em um espaço ambiental multidimensional e abstrato (RANGEL; LOYOLA, 2012;

BROENNINMAN *et al.*, 2012; DI COLA *et al.*, 2017; BROWN; CARNAVAL, 2019), com as vantagens, não só de comparar espécies ou populações distribuídas em diferentes geografias, mas também considerando o estado de não equilíbrio das suas áreas de distribuição (BROWN; CARNAVAL, 2019).

Estudos de modelagem de nicho ecológico em aves marinhas são um desafio, devido à falta de barreiras evidentes para dispersão (MELO-MERINO *et al.*, 2020). Particularmente, as costas da América do Sul, estão divididas em diferentes províncias costeiras que apresentam níveis distintos de produtividade marinha resultado da influência de diferentes correntes marinhas superficiais (OLSON *et al.*, 1988; WEICHLER *et al.*, 2004; THIEL *et al.*, 2007; SPALDING *et al.*, 2007), que podem oferecer alimento e influenciar os hábitos migratórios e reprodutivos das aves marinhas (BOST *et al.*, 2009; FRIEDLAENDER *et al.*, 2011) ou podem estar causando diferenciação morfológica e genética e estrutura populacional entre as espécies. Além disso, a maioria das aves marinhas são migratórias; movendo-se sazonalmente entre suas áreas reprodutivas e não reprodutivas, rastreando recursos alimentares e evitando condições climáticas adversas (DUFFY *et al.*, 2013; SOMVEILLE *et al.*, 2015; EYRES *et al.*, 2017; THROUP *et al.*, 2017). Em geral, faltam registros de ocorrência e dados ecológicos para estas espécies correspondentes às suas áreas não reprodutivas (PONTI *et al.*, 2020). Ainda, requerimentos bióticos, como a concentração de clorofila e disponibilidade de presas, e abióticas, como as oscilações da temperatura do mar, influenciam a distribuição de aves marinhas ao longo do ano (BARRETT; KRASNOV, 1996; WEICHLER *et al.*, 2004), aumentando a complexidade do procedimento de modelagem de nicho ecológico (EYRES *et al.*, 2017). Até agora, os estudos de modelagem de nicho ecológicos em aves marinhas têm sido realizados principalmente nas costas do Atlântico (MELO-MERINO *et al.*, 2020). Ainda faltam modelos com alta resolução temporal e espacial para maioria das espécies sul-americanas, particularmente aquelas que ocorrem nas costas do Pacífico (MELO-MERINO *et al.*, 2020).

4. A família Laridae

Laridae Rafinesque, 1815 (gaivotas, trinta-réis e afins) é uma família de aves marinhas que inclui cerca de 99 espécies, agrupadas em 23 gêneros (WINKLER *et al.*, 2020). Estão distribuídas em latitudes tropicais e temperadas nos dois hemisférios. A maioria das

espécies são migratórias, deslocando-se para regiões mais quentes durante o inverno (WINKLER *et al.*, 2020). Os larídeos ocupam uma ampla variedade de habitats, a maioria dos quais encontrados em áreas costeiras, outras espécies pelágicas passam a maior parte do ano no oceano, ou em ilhas costeiras, mas também podem encontrar-se em áreas lacustres e em rios (WINKLER *et al.*, 2020). Os hábitos alimentares também variam dentro da família, podendo ser consumidos uma variedade de itens. As gaivotas são oportunistas e alimentam-se de uma ampla variedade de presas; por exemplo, podem consumir desde pequenos mamíferos até ovos de outras espécies de aves e peixes (CALADO *et al.*, 2018). Por outro lado, os trinta-réis e afins costumam consumir principalmente peixes, crustáceos e insetos aquáticos (ALFARO *et al.*, 2011; WINKLER *et al.*, 2020). Adicionalmente, a maioria dos larídeos formam colônias (WINKLER *et al.*, 2020), i.e., agrupamentos de indivíduos em um sítio reprodutivo e apresentam ciclos de reprodução sincronizados dentro das colônias (COULSON, 2002). Em particular, algumas espécies de *Sterna* se reproduzem nas costas da América do Sul, como *Sterna trudeaui* (GOCHFELD *et al.* 2020a) e *Sterna hirundinacea* (BRANCO, 2003; PORTFLITT-TORO *et al.*, 2018). Outras espécies como *Sterna vittata*, *Sterna hirundo* e *Sterna paradisaea* são visitantes da América do Sul somente durante a sua época não reprodutiva (GOCHFELD *et al.*, 2020b; ARNOLD *et al.*, 2020; HATCH *et al.*, 2020). Finalmente, aproximadamente 22% das espécies de larídeos enfrentam alguma preocupação de conservação, devido a que suas populações estão sendo afetadas pela degradação dos seus habitats (WINKLER *et al.*, 2020). Em particular, o gênero *Sterna* é constituído atualmente por treze espécies (WINKLER *et al.*, 2020), quatro das quais são consideradas ameaçadas globalmente (BIRDLIFE INTERNATIONAL, 2022).

5. O trinta-réis-de-bico-vermelho *Sterna hirundinacea* Lesson, 1831

Sterna hirundinacea Lesson, 1831, trinta-réis-de-bico-vermelho, é uma espécie migratória da América do Sul, que está distribuída nas costas atlânticas, desde o sul do Brasil até à Argentina, incluindo as ilhas Malvinas/Falklands e na costa do Pacífico, no Chile, Peru e Equador. A espécie habita praias arenosas e rochosas, topos de penhascos e muitas vezes pequenas ilhas. O período reprodutivo das populações de trinta-réis-de-bico-vermelho varia de acordo com a latitude. Na costa do Brasil, ocorre entre abril e junho, enquanto no Chile, Uruguai e Argentina em outubro e dezembro (VOOREN; &

CHIARADIA, 1990; CARLOS, 2009; GOCHFELD *et al.*, 2020). As populações de trinta-réis-de-bico-vermelho localizadas no Sul apresentam uma migração direcional de longa distância (EYRES *et al.*, 2017; GOCHFELD *et al.*, 2020). No entanto, ainda não está claro se essas migrações de longa distância também são realizadas pelas populações do Norte.

A espécie tem um estado de conservação global “Pouco Preocupante”, porque apresenta uma ampla distribuição, um tamanho populacional moderado e sua população global parece não estar em declínio significativo (BIRDLIFE INTERNATIONAL, 2022). Porém, no Brasil, o trinta-réis-de-bico-vermelho é considerado como uma espécie “Vulnerável” (ICMBio, 2016) e suas populações são afetadas pela perturbação humana nos locais de nidificação (BIRDLIFE INTERNATIONAL, 2022; FARIA *et al.*, 2010; GOCHFELD *et al.*, 2020). Igualmente, as populações presentes nas costas do Chile também têm sido afetadas pela coleta ilegal de ovos (FARIA *et al.*, 2010; BIRDLIFE INTERNATIONAL, 2022; GOCHFELD *et al.*, 2020). Em outros países, como Argentina e Uruguai, a espécie é considerada como rara, com baixo tamanho populacional e distribuição reduzida ou restrita a alguma área em particular (AZPIROZ *et al.*, 2012; SOUTULLO *et al.*, 2013; PUGNALI *et al.*, 2016).

O estudo filogenético mais completo até agora realizado para o clado dos trinta-réis foi baseado em DNA mitocondrial, e agrupa *S. hirundinacea* como espécie irmã de *Sterna vittata* trinta-réis-antártico e *Sterna paradisaea* trinta-réis-ártico no gênero *Sterna* (BRIDGE *et al.*, 2005). Por outro lado, existe também um estudo molecular para a espécie (FARIA *et al.*, 2010). Esse trabalho sobre a estruturação genética das populações da costa Atlântica, baseado em marcadores mitocondriais e microssatélites, indica que parece existir uma baixa diferenciação genética entre as populações da costa Brasileira e da Patagônia. No entanto, não foram incluídos dados para as populações das Ilhas Malvinas/Falklands e do Pacífico (FARIA *et al.*, 2010). Outros estudos têm sido focados no comportamento reprodutivo (BRANCO, 2003; FRACASO, 2011; HOGAN *et al.*, 2010) e alimentar da espécie (ALFARO *et al.*, 2011; AJÓ *et al.*, 2011), mas também existem alguns poucos trabalhos sobre morfometria, sexagem e taxonomia (CARLOS; VOISIN, 2013; LISNIZER *et al.*, 2014).

Deste modo, os fatores que podem influir na diferenciação genética e morfológica entre as populações de trinta-réis-de-bico-vermelho não são totalmente conhecidos. As evidências comportamentais (migração e reprodução), genéticas e morfológicas recolhidas até ao momento são insuficientes para esclarecer se a espécie se divide em

linhagens evolutivas únicas, que precisariam de uma reavaliação de seus estados taxonômicos e de conservação. De acordo com este pressuposto postulamos as seguintes hipóteses:

Hipótese 1: Os fatores ecológicos e ambientais que delimitam as províncias marinhas costeiras influenciam espaço-temporalmente o nicho ecológico das comunidades de aves marinhas.

Predição: Espera-se encontrar também diferenças espaço-temporais no nicho ecológico entre as populações de trinta-réis-de-bico-vermelho. Essas diferenças serão observadas a partir da análise das curvas resposta das variáveis ambientais mais relevantes para o nicho ecológico e a distribuição da espécie.

Hipótese 2: O isolamento alocrônico e o comportamento migratório distinto entre as populações do trinta-réis-do-bico-vermelho distribuídas ao longo das províncias costeiras podem estar causando estrutura morfológica e genética.

Predição: Espera-se observar diferenças morfológicas e genéticas entre as populações de trinta-réis-de-bico-vermelho coincidente com as províncias marinho costeiras.

O presente estudo teve como objetivo geral avaliar a variação ecológica, morfológica e genética do trinta-réis-de-bico-vermelho para entender a estruturação populacional da espécie ao longo da sua área de ocorrência. Os objetivos específicos foram:

- 1- Estimar modelos de nicho ecológico em toda a área de distribuição da espécie por estação do ano, e em cada uma das populações delimitadas por requerimentos ambientais distintos;
- 2- Comparar os nichos ecológicos estimados entre áreas, estações reprodutivas e não reprodutivas, através de análises de diferenciação do espaço ambiental;
- 3- Descrever as variáveis ambientais mais relevantes para a distribuição da espécie;
- 4- Descrever os fatores que influenciam a variação morfológica na espécie.
- 5- Descrever os fatores que influenciam a estruturação genética nas trinta-réis-de-bico-vermelho;
- 6- Descrever a história demográfica das populações de trinta-réis-de-bico-vermelho com base em marcadores moleculares.

De modo geral, os resultados deste projeto indicam que a espécie não ocupa nichos ecológicos significativamente diferentes ao longo do ano, exceto durante a época de reprodução, particularmente entre as províncias do Pacífico Sudoeste Temperado Quente e do Atlântico Sudoeste Temperado Quente no outono. O comportamento migratório do trinta-réis-de-bico-vermelho, a seleção de diferentes microhabitats e áreas reprodutivas podem estar influenciando na diferenciação do espaço ambiental da espécie. Adicionalmente, os modelos de nicho ecológico reforçam a migração gradual desta espécie para o sul, passando o verão principalmente nas Ilhas Malvinas/Falkland.

Por outro lado, os dados morfológicos e genéticos indicam estrutura populacional limitada entre as populações do trinta-réis-de-bico-vermelho, com apenas alguma diferenciação no comprimento total da asa e da cauda para os espécimes da província temperada quente do Pacífico Sudeste. A forte conectividade migratória da espécie, seguida de seu comportamento não filopátrico, poderiam estar contribuindo para a manutenção do fluxo gênico entre suas populações.

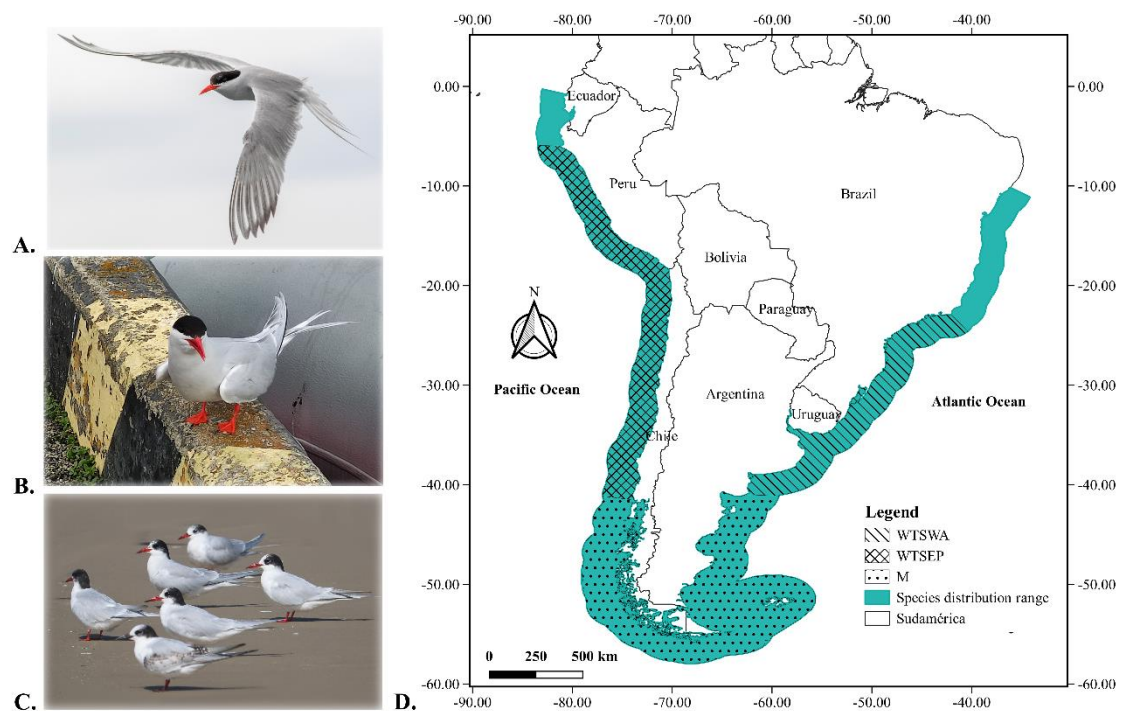


Figura 1. O trinta-réis-de-bico-vermelho *Sterna hirundinacea*: **A.** e **B.** correspondem, respectivamente, a um indivíduo com plumagem reprodutiva em voo e pousado em instalações industriais, **C.** Bando formado por um juvenil e indivíduos em plumagens não

reprodutiva e **D.** Distribuição geográfica da espécie (área azul). As linhas transversais e pontos pretos representam as províncias costeiras, segundo Spalding et al. (2007): Atlântico Sudoeste Temperado Quente (WTSWA), Magalhães (M) e Pacífico Sudoeste Temperado Quente (WTSEP). Fotografia **A.** Autor: Filipe Bernardi, Fotografia **B.** Autor: Rodrigo Araujo de Souza e Fotografia **C.** Autor: Maurício Tavares.

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CAPITULO 1

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

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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 behavior 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 behavior, 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.

ARTICLE INFO

Keywords: Coastal provinces, migration, niche overlap, niche divergence, niche truncation, seasonality.

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., 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 behavior 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 behavior 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 harbor 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), 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 behavior and particularly the different seasonally reproductive habits along the species distribution suggest the South American Tern might harbor 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°N to -58.6°S and longitude from -69.4°W to -33.3°E) and the Pacific coasts of South America (latitude from -0.14°N to -58.01°S and longitude from -84.2°W to -67.1°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 8,585 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 443nm, 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", "lqp", "q"), 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 ≤ 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= 50km`), 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 443nm, 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 (≤ 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 behavior 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 443nm 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 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, 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 between seasons presented between low to moderate niche truncation ($PNTI \leq 0.17$; 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 behavior is well evidenced in the records available for the Atlantic, particularly southern Argentina, with considerably 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 marinii*, *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*, Stripped 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 clupeola*; 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 (Güet et al., 2019), coinciding with the species migratory behavior. Additionally, the South American Tern can occasionally exploit other resources (Alfaro et al., 2011). 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 behavior 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 *Sterna paradisaea*, encompass coastal, oceanic and polar regions (Duffy et al., 2013; Fijn et al., 2013; Redfern and Bevan, 2020); and the Common Tern *Sterna hirundo* 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 among 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.

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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.

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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
			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	

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 ₁₋₂	B ₂₋₁	D	E	B ₁₋₂	B ₂₋₁	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	15	0	0.95	**	**	-	-	-	-	-	0.24	0.03
Spring	57	Fall	23	0.01	1	0.25	0.37	0.03	1	0.96	0.16	61.7	0.09	0.11
WTSEP	23	WTSWA	15	0.01	*	0.52	0.91	0.04	0.97	**	*	80.8	0.08	0
Fall	23	Fall	57	0.09	1	*	**	0.11	1	0.15	**	71.4	0.07	0.09
WTSEP	23	M	57	0.02	1	*	0.90	-	-	-	-	-	0.32	0
Spring	14	Spring	12	0.04	1	**	0.89	0.00	0.32	0.70	0.08	62.2	0.08	0
WTSWA	23	M	12	0.01	0.98	*	0.97	-	-	-	-	-	0.08	0
Fall	15	Fall	12											

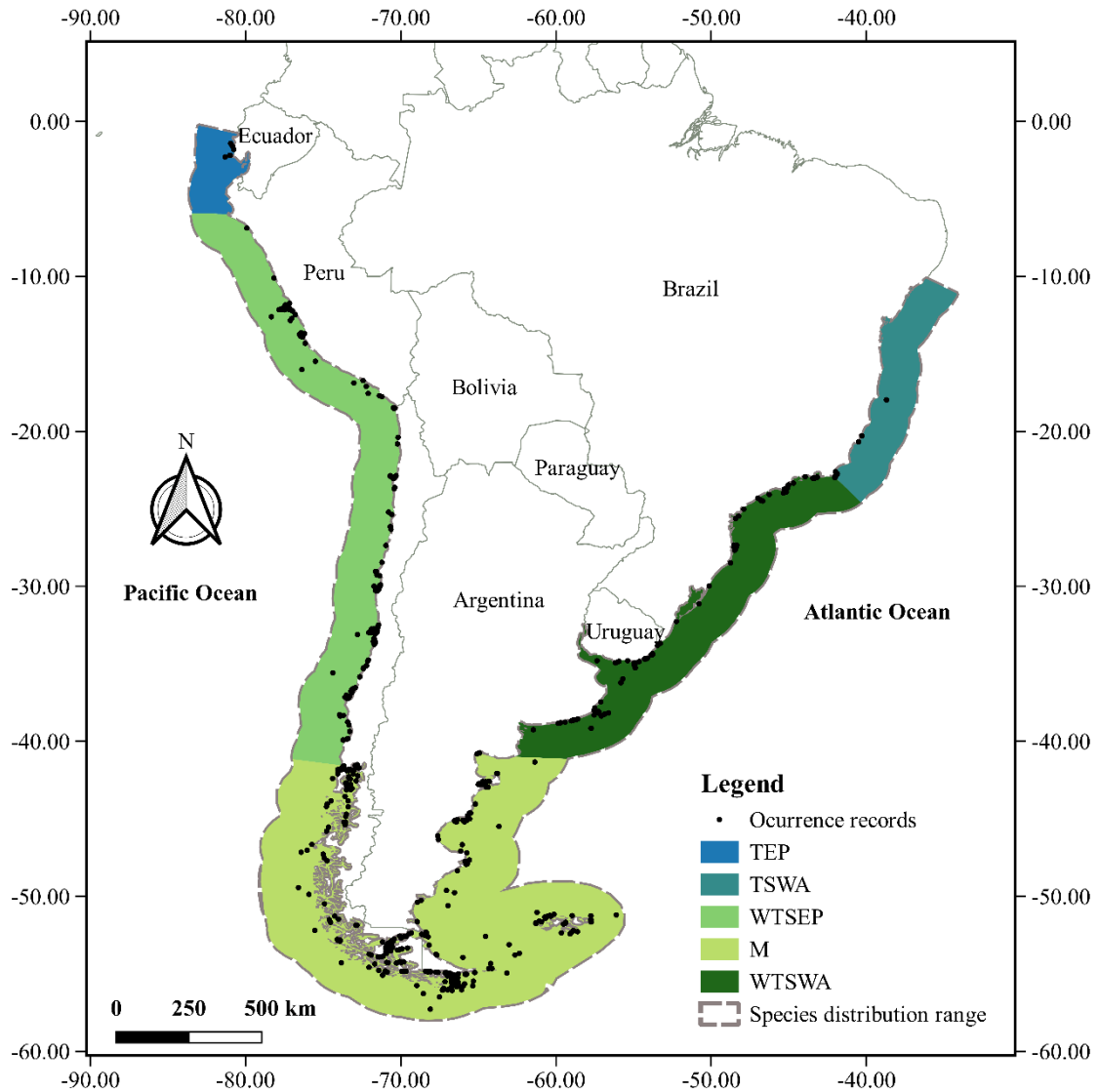


Fig. 1. Calibration area for the South America Tern *Sterna hirundinacea* models and distribution of the occurrence records used. Colored areas represent coastal provinces following the Global Biogeographic System for Coastal and Shelf Areas, Marine Regions of the World (Spalding et al., 2007): Warm Temperate Southwestern Atlantic (WTSWA), Magellanic (M), Warm Temperate Southeastern Pacific (WTSEP), Tropical Eastern Pacific (TEP) and the Tropical Southeastern Atlantic (TSWA).

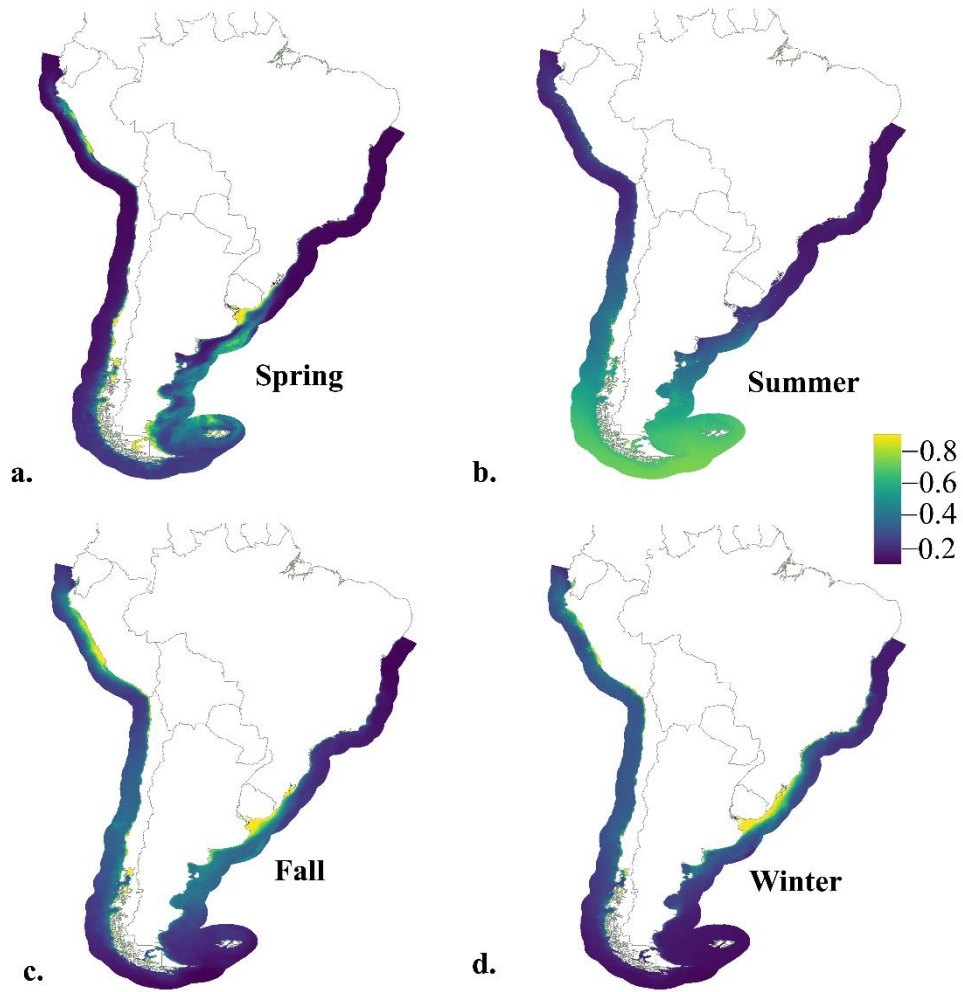


Fig. 2. Occurrence probability for the South America Tern *Sterna hirundinacea* under the first modelling approach: a. spring, b. summer, c. fall and d. winter.

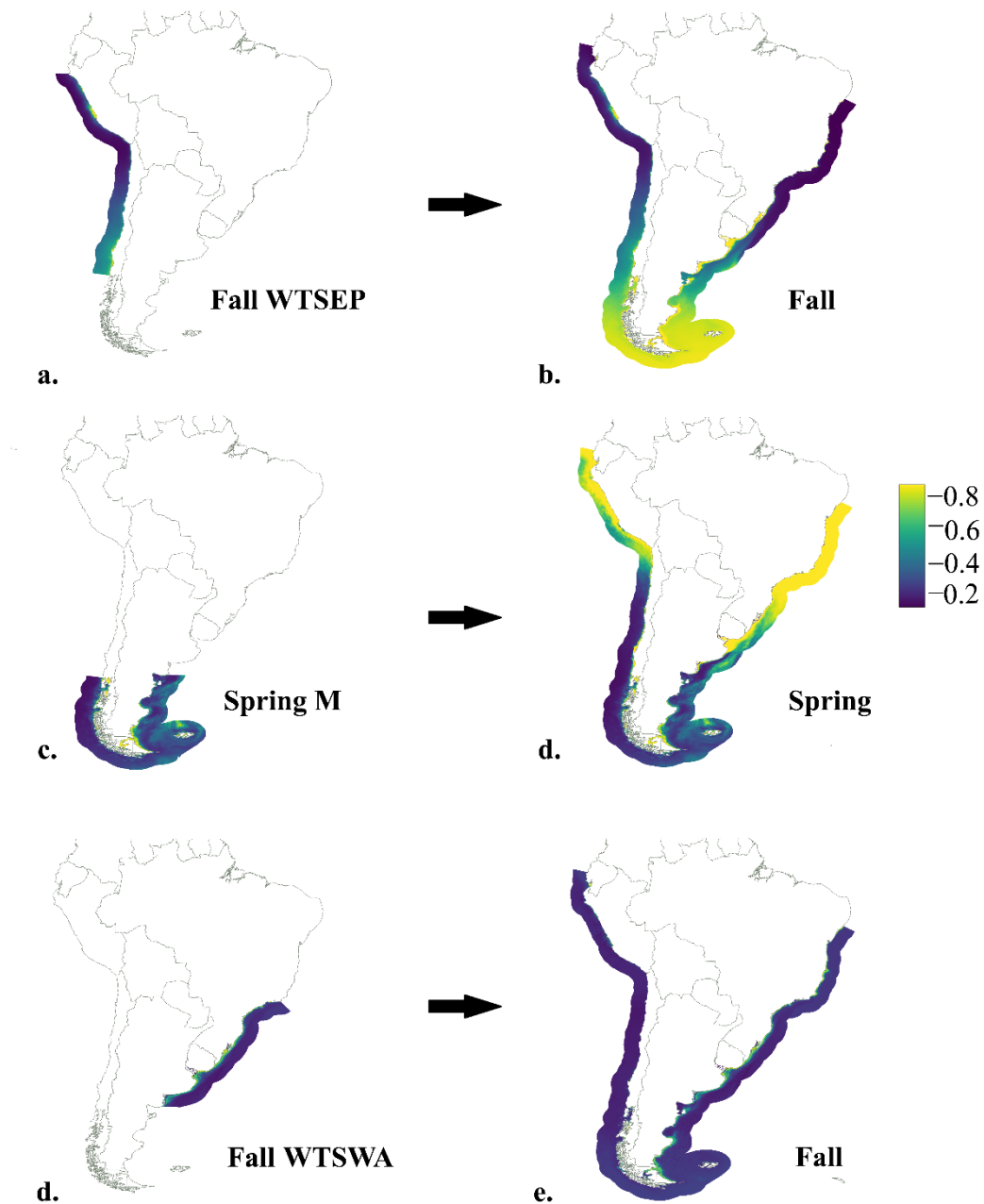


Fig. 3. Occurrence probability for the South America Tern *Sterna hirundinacea* projections using Maxent algorithm. The models were calibrated using records for each breeding area per season, and projected to the entire species distribution range. The three calibration areas corresponded to the Warm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

Supplementary Material

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

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This document includes:

Table S1. List of occurrence records

Table S2. Description of the Ecological niche models following the ODMAP protocol

Fig. S1. Plots of the number of occurrence records used per year and season

Fig. S2. Plots for the mean annual values for each environmental variable

Fig. S3. Response curves for the environmental variables

Appendix S1. R code

Table S1. List of occurrence records of the South American Tern *Sterna hirundinacea* used in this study. The season when the record was collected, as well as the geographic coordinates and verbatim locality for each record, are informed.

Season	Longitude	Latitude	Locality
Spring	-80.76	-1.82	Montañita Beach, Santa Elena Province, Ecuador
Spring	-81.01	-2.19	La Chocolatera, Salinas, Santa Elena Province, Ecuador
Spring	-77.27	-12.10	San Lorenzo Island, Callao, Callao Province, Peru
Spring	-77.84	-12.15	Lima, Lima Province, Peru
Spring	-76.80	-12.48	Port Puscusana, Lima Province, Peru
Spring	-76.98	-12.22	Villa Wildlife Refuge, Pampas Mojadas, Lima Province, Peru
Spring	-73.03	-16.88	Camaná Province, Arequipa Department, Peru
Spring	-77.67	-12.12	Near to Hormigas de Afuera Island, Callao Province, Peru
Spring	-72.43	-16.72	Quilca, Camaná Province, Arequipa Department, Peru
Spring	-77.22	-12.04	Near to San Lorenzo Island, Callao Province, Peru
Spring	-76.40	-13.74	Ballestas Islands, Pisco Province, Peru
Spring	-77.33	-12.06	Near to San Lorenzo Island Callao Province, Peru
Spring	-77.39	-12.05	Near to San Lorenzo Island Callao Province, Peru
Spring	-77.55	-12.01	Near to San Lorenzo Island Callao Province, Peru
Spring	-78.34	-12.61	Shelf west of Callao, Callao region, Peru
Spring	-76.42	-13.63	Chincha Islands, Ica Department, Peru
Spring	-76.21	-13.68	Mouth of Pisco River, Ica Department, Peru
Spring	-71.63	-33.03	Valparaiso, Valparaiso region, Chile
Spring	-71.95	-33.00	Valparaiso, Valparaiso region, Chile
Spring	-70.90	-53.17	Punta Arenas, Magellan and the Chilean Antarctic Region, Chile
Spring	-70.68	-53.23	Punta Arenas, Magellan and the Chilean Antarctic Region, Chile
Spring	-71.63	-33.62	Maipo River, Valparaiso region, Chile
Spring	-67.26	-55.96	Hornos Island, Magellan and the Chilean Antarctic Region, Chile
Spring	-67.23	-55.96	Cape Horn, Magellan and the Chilean Antarctic Region, Chile
Spring	-70.58	-52.92	Magdalena Island, Magellan and the Chilean Antarctic Region, Chile
Spring	-71.58	-32.77	Seno de Reloncavi, Valparaiso region, Chile

Season	Longitude	Latitude	Locality
Spring	-72.88	-41.57	Seno de Reloncavi, Los Lagos, Chile
Spring	-70.38	-18.50	Arica, Arica and Paranicota, Chile
Spring	-71.46	-53.91	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Spring	-71.28	-53.91	Strait of Magellan, Magellan and Chilean Antarctica region, Chile
Spring	-71.13	-53.87	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Spring	-70.91	-53.68	London Island, Magellan and the Chilean Antarctic Region, Chile
Spring	-72.05	-54.58	Chile
Spring	-70.94	-53.65	San Juan, Caquén Colorado Reserve, Chile
Spring	-73.35	-41.81	Calbuco, Los Lagos region, Chile
Spring	-70.67	-26.15	El Soldado Beach, Pan de Azúcar National Park, Chile
Spring	-70.63	-53.25	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Spring	-65.96	-55.76	Cape Horn, Magellan and Chilean Antarctic region, Chile
Spring	-65.35	-55.78	Drake passage, Magellan and the Chilean Antarctic Region, Chile
Spring	-70.07	-52.57	Estancia San Gregorio, Punta Arenas, Magellan and the Chilean Antarctic Region, Chile
Spring	-71.76	-32.98	Valparaiso, Valparaiso region, Chile
Spring	-70.45	-18.51	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Spring	-70.18	-53.46	Inútil Bay, Tuququere, Magellan and the Chilean Antarctic Region, Chile
Spring	-70.08	-53.44	Magellan and the Chilean Antarctic Region, Chile
Spring	-74.06	-42.10	Ahuenco park, Chiloé, Los Lagos region, Chile
Spring	-67.13	-54.93	Beagle channel, Chile
Spring	-71.70	-33.43	Punta de Tralca, Valparaiso region, Chile
Spring	-65.89	-55.65	Mouth of the Beagle Channel, Chile

Season	Longitude	Latitude	Locality
Spring	-66.82	-55.98	Near to Deceit Island, Magellan and the Chilean Antarctic Region, Chile
Spring	-66.39	-55.84	Near to Deceit Island, Magellan and the Chilean Antarctic Region, Chile
Spring	-68.10	-57.28	Drake Passage, Chile
Spring	-70.57	-52.85	Marta Island, Punta Arenas, Magellan and the Chilean Antarctic Region, Chile
Spring	-68.66	-52.45	Strait of Magellan, Magellan and the Chilean Antarctic Region Antarctic Region, Chile
Spring	-71.36	-29.95	Coquimbo, Elqui Province, Chile
Spring	-70.88	-54.89	Near to Stewart Island, Magellan and the Chilean Antarctic Region, Chile
Spring	-71.51	-30.28	Tongoy, Salinas Chicas, Coquimbo region, Chile
Spring	-71.61	-33.04	Near to Stewart Island, Magellan and The Chilean Antarctic Region Antarctic Region, Chile
Spring	-71.55	-32.99	Salinas Beach, Viña del Mar, Valparaiso Province, Chile
Spring	-71.38	-30.07	Totalillo Beach, Coquimbo, Elqui Province, Chile
Spring	-73.23	-42.77	Near to Desertores Island, Los Lagos region, Chile
Spring	-70.94	-53.57	Port del Hambre, ruta Ch-9, Magellan and The Chilean Antarctic Region, Chile
Spring	-71.53	-32.78	Seno de Reloncavi, Valparaiso region, Chile
Spring	-74.06	-52.84	Magellan and the Chilean Antarctic Region, Chile
Spring	-72.69	-41.71	Near to Port Montt, Llanquihue Province, Los Lagos region, Chile
Spring	-71.30	-29.93	Coquimbo Bay, Coquimbo region, Chile
Spring	-70.87	-53.14	Punta Arenas, Magellan and the Chilean Antarctic Region, Chile
Spring	-71.37	-29.98	La herradura Beach, Coquimbo region, Chile
Spring	-70.67	-53.03	El Soldado Beach, Pan de Azucar National Park, Chile
Spring	-70.75	-53.26	Magellan and Chilean Antarctica region, Chile
Spring	-71.75	-33.01	Valparaiso, Valparaiso region, Chile
Spring	-70.94	-53.23	Lenadura, Punta Arenas, Magellan and the Chilean Antarctic Region, Chile

Season	Longitude	Latitude	Locality
Spring	-66.69	-56.08	Cape Horn at sea, Chilean Antarctica Province, Chile
Spring	-66.77	-55.89	Cape Horn, Magellan and the Chilean Antarctic Region, Chile Hornos Island, Magellan and the Chilean Antarctic Region,
Spring	-67.31	-56.06	Chile
Spring	-71.49	-30.25	Mouth of Estero Tongoy, Coquimbo region, Chile
Spring	-70.42	-23.70	Antofasta Beach, Antofasta Province, Antofasta region, Chile
Spring	-77.49	-12.16	Cape Horn, Magellan and The Chilean Antarctic Region, Chile Fuerte Bulnes, Strait of Magellan, Magellan and the Chilean
Spring	-70.91	-53.63	Antarctic Region, Chile
Spring	-66.08	-56.03	Drake Passage and nearing Beagle Channel, Chile
Spring	-70.46	-18.50	Arica Province, Arica and Paranicota region, Chile
Spring	-67.00	-55.14	Beagle channel, Chile
Spring	-75.73	-46.65	Near to the Taitao Peninsula, Aysén region, Chile
Spring	-72.88	-42.55	Desamparaos Channel, Los Lagos region, Chile
Spring	-73.47	-39.85	Morro Gonzalo, Valdivia Province, Los Lagos region, Chile Strait of Magellan, Magellan and the Chilean Antarctic Region,
Spring	-70.67	-53.19	Chile
Spring	-66.76	-55.06	Near to Picton Island, Beagle Channel, Chile
Spring	-71.46	-32.58	Cachagua Peninsula, Valparaiso region, Petorca Province, Chile
Spring	-71.79	-32.81	Seno de Reloncavi, Valparaiso Province, Chile
Spring	-73.59	-43.56	Gulf of Corcovado, Los Lagos region, Chile Diego Ramírez Islands, Magellan and The Chilean Antarctic
Spring	-68.54	-56.28	Region, Chile
Spring	-71.73	-29.99	La Serena, Coquimbo region, Chile
Spring	-72.90	-41.65	Port Montt, Llanquihue Province, Los Lagos region, Chile Strait of Magellan, Between Carlos III Island and Cape Froward,
Spring	-71.90	-53.79	Chile Richmond Strait, between Lennox Island and Nueva Island,
Spring	-66.76	-55.25	Chile
Spring	-70.30	-22.87	North of Hornito, Antofasta region, Chile Highway 9, Punta Arenas, San Juan River, Magellan and the
Spring	-70.96	-53.37	Chilean Antarctic Region, Chile

Season	Longitude	Latitude	Locality
Spring	-73.41	-39.83	Centinillo, Valdivia Province, Chile
Spring	-69.92	-53.39	Inutil Bay, Magellan and The Chilean Antarctic Region, Chile
Spring	-70.45	-18.48	Arica Province, Arica and Paranicota region, Chile
Spring	-72.75	-41.71	Seno de Reloncavi, Piconya, Los Lagos region, Chile
Spring	-71.61	-30.29	Port Aldea, Coquimbo region, Chile
Spring	-73.03	-41.88	North of Gulf of Ancud, Los Lagos region, Chile
Spring	-72.78	-42.22	Punta Quillon, Los Lagos region, Chile
Spring	-71.44	-32.50	Papudo, Atacama region, Chile
Spring	-71.62	-29.04	Chañaral Island, Atacama region, Huasco Province, Chile
Spring	-72.79	-33.11	Nautical crossing San Fernandez, Valparaiso region, Chile
Spring	-72.93	-41.57	Near to Maillen Island Los Lagos region, Chile
Spring	-66.46	-55.68	Cape Horn, Magellan and the Chilean Antarctic Region, Chile
Spring	-73.23	-43.11	Quellón to Chaitan ferry, Los Lagos region, Chile
Spring	-66.65	-55.75	Vavilov, Chilean sea, Chile
Spring	-66.92	-54.96	Vavilov, Chilean sea, Chile
Spring	-73.17	-36.81	Mouth of the Biobío River, Biobío region, Chile
Spring	-70.53	-53.30	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Spring	-70.06	-54.22	Seno Almirantazgo, Karukinka natural park, Tierra del fuego region, Chile
Spring	-70.28	-54.31	Seno Almirantagoza, Alberto de Agostini National Park, Magellan and the Chilean Antarctic Region, Chile
Spring	-71.00	-54.82	Ballenero channel, Alberto de Agostini National Park, Magellan and the Chilean Antarctic Region, Chile
Spring	-71.64	-33.58	San Antonio Province, Chile
Spring	-74.06	-41.83	Puñihuil, Chiloé Province, Los Lagos region, Chile
Spring	-71.43	-30.20	Guanaqueros, Elqui Province, Coquimbo region, Chile
Spring	-73.72	-39.91	Chaihuin, Valdivia Province, Los Rios region, Chile
Spring	-71.90	-32.76	Seno de Reloncavi, Valparaiso Province, Valparaiso region, Chile
Spring	-73.29	-39.36	Queule, Cautin Province, Araucania region, Chile
Spring	-73.34	-38.94	Puaucho Beach, Araucania region, Chile

Season	Longitude	Latitude	Locality
			70 km north along shore of Ancha Beach, Valparaiso region,
Spring	-71.67	-33.02	Chile
Spring	-70.73	-53.22	Punta Arenas to Tierra del fuego, Chile
Spring	-71.63	-33.00	Valparaiso, Valparaiso region, Chile
Spring	-71.67	-32.72	Seno de Reloncavi, Valparaiso region, Chile
Spring	-68.97	-55.76	Southwest off Tierra del Fuego, Chile
Spring	-71.87	-32.76	Fifteen miles off Seno de Reloncavi, Valparaiso region, Chile
Spring	-60.54	-51.29	Carcass Island, Malvinas/Falkland Islands
Spring	-59.10	-52.43	Sea Lion Island Malvinas/Falkland Islands
Spring	-61.22	-51.04	Steeple Jason Island Malvinas/Falkland Islands
Spring	-61.31	-51.74	New Island South rookery, Malvinas/Falkland Islands
Spring	-57.73	-51.66	Channel leaving Stanley, Malvinas/Falkland Islands
Spring	-58.88	-52.22	Bleaker Island, Malvinas/Falkland Islands
Spring	-60.56	-51.30	Carcass Island, Malvinas/Falkland Islands
Spring	-60.67	-51.38	Zodiac into West Point Island, Malvinas/ Falkland Islands
Spring	-60.69	-51.43	South of West Point Island, Malvinas/ Falkland Islands
Spring	-57.75	-51.51	Volunteer point, Soledad Island, Malvinas/ Falkland Islands
Spring	-59.39	-51.74	Malvinas/ Falkland Islands
Spring	-59.07	-52.42	Sea Lion Island, Malvinas/Falkland Islands
			Atlantic Ocean, 36 nautical miles east of Stanley, Malvinas/
Spring	-56.11	-51.20	Falkland Islands
Spring	-63.02	-53.12	South West of Malvinas/ Falkland Islands
Spring	-58.61	-52.28	Sea Lion Island, Malvinas/Falkland Islands
Spring	-56.88	-38.25	Mar del Plata, Buenos Aires Province, Argentina
Spring	-64.31	-42.58	Punta Pirámides, Valdés Peninsula, Patagonia region, Argentina
Spring	-58.98	-38.67	Punta Florida, Buenos Aires Province, Argentina
			Balneario Los Angeles, Necochea, Buenos Aires Province,
Spring	-59.01	-38.68	Argentina
			Punta Popper Urban Nature Reserve, Tierra del Fuego Province,
Spring	-67.67	-53.79	Argentina
			Protected Natural Area Punta Loma, Chubut Province,
Spring	-64.89	-42.81	Argentina

Season	Longitude	Latitude	Locality
Spring	-68.42	-52.39	Punta Dungeness, Santa Cruz Province, Argentina
Spring	-68.94	-51.66	Marjory Glenn, Santa Cruz Province, Argentina
Spring	-66.35	-48.36	Cape Guardian, Laura bay, Santa Cruz Province, Argentina Monte León National park, Punta indice, Aonikenk roch,
Spring	-68.69	-50.27	Argentina
Spring	-65.00	-42.78	Port Madryn, Chubut Province, Argentina
Spring	-65.74	-45.09	Marino Costero Patagonia Austral Park, Argentina Observatorio Island, Tierra del Fuego region, Antarctica and
Spring	-64.13	-54.66	Atlantic south Islands Province, Argentina
Spring	-58.59	-38.56	Buenos Aires Province, Argentina
Spring	-65.87	-47.75	Estuary of Deseado River, Santa Cruz Province, Argentina Espigon pescadores ecolic park, Nechochea, Buenos Aires
Spring	-58.79	-38.61	Province, Argentina
Spring	-55.82	-36.22	San Clemente del Tuyú, Buenos Aires Province, Argentina
Spring	-66.95	-50.60	Grande bay, Santa Cruz Province, Argentina Pinguino Island, Puerto Deseado, Santa Cruz Province,
Spring	-65.72	-47.91	Argentina
Spring	-63.17	-54.95	At sea near to the East of Beagle channel, Argentina
Spring	-63.76	-42.08	Valdés Peninsula, Punta Norte, Chubut Province, Argentina Faro Querandí Nature Reserve, Buenos Aires Province,
Spring	-57.11	-37.46	Argentina
Spring	-68.36	-52.34	Cape Virgenes Nature Reserve, Santa Cruz Province, Argentina
Spring	-68.18	-53.15	Ushuaia bay, Beagle channel, Argentina
Spring	-66.54	-45.13	Bustamante bay, Chubut Province, Argentina
Spring	-65.74	-47.20	Cape Blanco Nature Reserve, Santa Cruz Province, Argentina
Spring	-64.38	-42.95	El Pedral Beach, Chubut Province, Argentina Caves of Monte León, Monte León National Park, Santa Cruz
Spring	-68.92	-50.38	Province, Argentina
Spring	-65.56	-45.00	Aguilán del Sur Island, Chubut Province, Argentina
Spring	-64.53	-42.60	Port Pyramids, Chubut Province, Argentina
Spring	-62.36	-53.68	Between Staten Island and Falkland Islands, Argentina
Spring	-66.04	-46.67	Gulf of San Jorge, Santa Cruz Province, Argentina

Season	Longitude	Latitude	Locality
Spring	-66.54	-49.77	Argentine sea, Santa Cruz Province, Argentina
Spring	-61.36	-41.34	Argentine sea, Rio Negro Province, Argentina
Spring	-65.90	-45.20	Argentine sea, Chubut Province, Argentina
Spring	-65.58	-47.66	Puerto Deseado, Santa Cruz Province, Argentina
Spring	-65.08	-40.82	Las Grutas, Rio Negro Province, Argentina
			Los Estados Island, Tierra del fuego region, Antarctica and the
Spring	-64.33	-54.66	South Atlantic Island Province, Argentina
Spring	-55.70	-35.97	Samborombón bay, Buenos Aires Province, Argentina
			Pinguino Island, Puerto Deseado, Santa Cruz Province,
Spring	-65.83	-47.80	Argentina
			From Necochea to Los Angeles, Buenos Aires Province,
Spring	-58.87	-38.64	Argentina
Spring	-62.64	-53.79	At sea, Tierra del Fuego region, Argentina
Spring	-64.71	-42.60	Port Madryn, Chubut Province, Argentina
Spring	-54.95	-34.97	Punta del Este, Uruguay
Spring	-55.95	-34.84	Solymar, Ciudad de la Costa, Uruguay
Spring	-55.38	-34.80	Costa Azul, Canelones Department, Uruguay
Spring	-53.79	-34.35	Cape Polonio, Rocha Department, Uruguay
Spring	-53.87	-34.43	Cape Polonio, Sur Beach, Rocha Department, Uruguay
Spring	-54.28	-34.68	Barra of the Rocha Lagoon, Rocha Department, Uruguay
Spring	-53.78	-34.41	Cape Polonio, Rocha Department, Uruguay
Spring	-54.16	-34.67	La Paloma, Rocha Department, Uruguay
			Mouth of the Arroyo de Chuy, 10km south, Rocha Department,
Spring	-53.45	-33.81	Uruguay
Spring	-56.16	-34.94	Montevideo, Montevideo Department, Uruguay
Spring	-54.12	-34.65	La Paloma, Rocha Department, Uruguay
Spring	-52.24	-32.27	Casino Beach, Rio Grande do Sul State, Brazil
Spring	-48.43	-25.64	Pontal do Paraná, Paraná State, Brasil
			Manguezal de Ratones, Daniela Beach, Florianópolis, Santa
Spring	-48.54	-27.45	Catarina State, Brazil
Spring	-48.37	-27.46	Santinho Beach, Florianópolis, Santa Catarina State, Brazil
Spring	-42.04	-22.96	Arrial do Cabo, Rio de Janeiro State, Brazil

Season	Longitude	Latitude	Locality
Spring	-43.32	-23.01	Near to Windsor Barra Hotel, Rio de Janeiro State, Brazil
Summer	-77.84	-12.15	Lima Province, Peru
Summer	-77.21	-12.12	Natural reserve of Cavinzase Island, Peru
Summer	-70.63	-53.25	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Summer	-73.07	-42.10	Gulf Ancud, Los Lagos region, Chile
Summer	-71.63	-33.62	Mouth of Maipo River, Valparaiso region, Chile
Summer	-70.94	-53.65	San Juan, Caquén Colorado Reserve, Chile
Summer	-71.95	-33.00	Valparaiso region, Chile
Summer	-70.68	-53.23	Strait of Magellan, between Punta Arenas and Porvenir, Chile
Summer	-66.50	-55.14	Beagle Channel, Chile
Summer	-73.91	-52.82	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Summer	-66.71	-55.45	Drake Passage and nearing Beagle Lennox Island, Chile
Summer	-70.94	-53.57	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Summer	-72.04	-53.73	Strait of Magellan, near to Carlos III Island, Magellan and the Chilean Antarctic Region, Chile
Summer	-70.67	-52.96	Strait of Magellan, near to Magdalenas Island, Magellan and the Chilean Antarctic Region, Chile
Summer	-73.38	-44.23	Moradela Channel, Aysén Province, Chile
Summer	-70.87	-53.14	Punta Arenas, Magellan and the Chilean Antarctic Region, Chile
Summer	-73.41	-37.07	Near to Santa Maria Island, Arauco Province, Biobío region, Chile
Summer	-73.36	-42.34	Tenuan, Los Lagos region, Chile
Summer	-70.83	-53.03	Chabunco, Magellan and the Chilean Antarctic Region, Chile
Summer	-73.21	-36.77	La Piedra, Hualpén Province, Biobío region, Chile
Summer	-71.68	-54.37	Cockburn channel, near to Alberto de Agustini National Park, Chile
Summer	-70.65	-53.51	Strait of Magellan, Magellan and The Chilean Antarctic Region, Chile
Summer	-76.42	-47.16	Gulf of Penas, Patagonia region, Chile

Season	Longitude	Latitude	Locality
Summer	-74.66	-45.53	Darwin Bay, Aysén region, Chile
Summer	-67.14	-54.95	Near to Snipe Island, Beagle Channel, Chile
Summer	-66.73	-55.57	Near to Evout Island, Magellan and the Chilean Antarctic Region, Chile
Summer	-69.46	-52.42	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Summer	-69.80	-54.24	Whiteside channel, Magellan and the Chilean Antarctic Region, Chile
Summer	-73.92	-52.90	Emiliano Figueroa Island, Magellan and the Chilean Antarctic Region, Chile
Summer	-70.89	-53.19	Offshore from Punta Arenas, Magellan and the Chilean Antarctic Region, Chile
Summer	-71.43	-54.78	Western approach to Beagle Channel, Chile
Summer	-71.40	-53.92	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Summer	-69.94	-52.63	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Summer	-70.91	-53.63	Bulnes Fort, Magellan and the Chilean Antarctic Region, Chile
Summer	-73.42	-38.76	Mouth of Imperia River, Cautin Province, Araucanía region, Chile
Summer	-74.74	-44.04	Chile
Summer	-72.90	-41.58	At sea, Aysén region, Chile
Summer	-74.49	-43.85	Near to Port Montt, Los Lagos region, Chile
Summer	-68.21	-54.85	Southeast of Guafo Island, Los Lagos region, Chile
Summer	-76.03	-47.03	Beagle Channel, Chile
Summer	-73.94	-38.29	Gulf Penas, Patagonia region, Chile
Summer	-73.59	-45.39	Mocha Island Natural reserve, Arauco Province, Biobío region, Chile
Summer	-70.47	-23.05	Chaculay Island, Rodriguez channel, Patagonia, Chile
Summer	-71.49	-30.25	Mejillones Bay, Antofasta Province, Chile
Summer	-72.80	-41.51	Mouth of Estero Togoy, Coquimbo region, Chile
Summer	-76.60	-49.44	Chamiza, Port Montt, Los Lagos region, Chile
Summer			Bernardo O'Higgins Natural Park, Patagonia region, Chile

Season	Longitude	Latitude	Locality
Summer	-71.70	-33.03	Ancha Beach, Valparaiso region, Chile
			Mouth of Gabriel channel, Magellan and the Chilean Antarctic
Summer	-70.26	-54.31	Region, Chile
			Broke channel, Timaukel, Magellan and the Chilean Antarctic
Summer	-69.97	-54.28	Region, Chile
Summer	-70.97	-53.37	Agua fresca, sector Santa Maria River, Strait of Magellan, Chile
Summer	-74.37	-35.58	Curanipe, Maule region, Chile
Summer	-73.14	-43.04	Gulf Corcovado, Quellón, Chile
Summer	-66.39	-55.13	Mouth of Beagle Channel, Chile
Summer	-71.76	-32.98	Valparaiso region, Chile
Summer	-70.38	-18.50	Arica Province, Arica and Paranicota region, Chile
Summer	-73.90	-41.79	Guapilacuy Bay, Los Lagos region, Chile
Summer	-72.21	-35.12	Mount of Huenchullami River, Maule, Chile
Summer	-71.58	-32.77	Seno de Reloncavi, Valparaiso Province, Chile
			Mocha Island natural reserve, Arauco Province, Biobío region,
Summer	-73.91	-38.36	Chile
Summer	-66.43	-55.36	Nueva Island, Magellan and the Chilean Antarctic Region, Chile
Summer	-66.98	-56.03	Cape Horn, Magellan and the Chilean Antarctic Region, Chile
Summer	-66.54	-55.57	Drake Passage and nearing Beagle Channel, Chile
Summer	-66.62	-55.70	Drake Passage and nearing Beagle Channel, Chile
Summer	-66.59	-55.64	Drake Passage and nearing Beagle Channel, Chile
Summer	-66.56	-55.59	Drake Passage and nearing Beagle Channel, Chile
Summer	-66.65	-55.76	Drake Passage and nearing Beagle Channel, Chile
Summer	-66.29	-55.66	Drake Passage and nearing Beagle Channel, Chile
Summer	-66.28	-55.74	Drake Passage and nearing Beagle Channel, Chile
Summer	-66.30	-55.56	Drake Passage and nearing Beagle Channel, Chile
			Near to Magdalena Island, Strait of Magellan, Magellan and the
Summer	-70.63	-52.98	Chilean Antarctic Region, Chile
Summer	-66.36	-55.18	Nueva Island, Drake Passage and nearing Beagle Channel, Chile
Summer	-73.50	-43.14	Punta Chaigua, Quellón, Chiloé Province, Chile
Summer	-73.09	-36.64	Tumbes, Talcahuano, Biobío region, Chile
Summer	-71.62	-33.04	Valparaiso region, Chile

Season	Longitude	Latitude	Locality
Summer	-70.57	-53.30	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Summer	-71.70	-32.95	Valparaiso region, Chile
Summer	-70.71	-53.03	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Summer	-70.62	-53.25	Porvenir, Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Summer	-71.21	-28.45	Huasco, Atacama region, Chile
Summer	-71.60	-32.82	Seno de Reloncavi, Valparaiso Province, Chile
Summer	-71.55	-32.96	Montermart rock, Viña del Mar, Chile
Summer	-73.59	-43.56	Gulf Corcovado, Quellón, Chile
Summer	-70.57	-52.85	Marta Island, Punta Arenas, Magellan and the Chilean Antarctic Region, Chile
Summer	-72.82	-51.87	Gulf Almirante Montt, Magellan and the Chilean Antarctic Region, Chile
Summer	-73.40	-43.85	Gulf Corcovado, Quellón, Chile
Summer	-67.67	-54.91	Port Williams, Beagle Channel, Chile
Summer	-72.64	-35.84	Curanipe, Maule region, Chile
Summer	-70.91	-54.27	Magdalena Channel, Magellan and the Chilean Antarctic Region, Chile
Summer	-69.74	-54.85	Italia Glacier, Beagle Channel, Alberto de Agostini National Park, Chile
Summer	-72.89	-51.86	Angustura white, Gulf Almirante Montt, Chile
Summer	-70.67	-22.86	Mejillones, Antofasta Province, Chile
Summer	-66.76	-55.06	Picton Island, Beagle Channel, Chile
Summer	-70.67	-22.90	Punta de Cuartel, Antofasta Province, Chile
Summer	-70.42	-23.69	Mejillones, Antofasta Province, Chile
Summer	-71.34	-29.93	Fuerte Lambert, Coquimbo region, Chile
Summer	-66.33	-55.25	Nueva Island, Mouth of Beagle Channel, Chile
Summer	-74.78	-45.80	Bracey Island, Magellan and the Chilean Antarctic Region, Chile
Summer	-70.96	-27.36	La Virgen Beach, Atacama, Chile

Season	Longitude	Latitude	Locality
Summer	-73.66	-45.22	Moralada Channel, Magellan and the Chilean Antarctic Region, Chile
Summer	-70.43	-23.02	Mejillones, Antofasta Province, Chile
Summer	-70.67	-53.19	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Summer	-70.50	-23.04	Punta Rieles, Mejillones, Antofasta Province, Chile
Summer	-71.54	-29.27	Choros Island, Pinguinos National Reserve, Chile
Summer	-70.73	-53.07	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Summer	-70.93	-53.31	Punta Arenas, Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Summer	-70.66	-53.02	Magdalena Island Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Summer	-67.60	-54.91	Port Williams, Beagle channel, Chile
Summer	-69.64	-52.58	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Summer	-69.98	-52.68	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Summer	-69.33	-52.36	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Summer	-69.78	-52.60	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Summer	-70.48	-52.89	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Summer	-70.43	-52.76	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Summer	-75.92	-49.87	Mornington Island, Magellan and the Chilean Antarctic Region, Chile
Summer	-74.53	-51.68	Amalia glacier, Punta Arenas, Magellan and the Chilean Antarctic Region, Chile
Summer	-75.00	-47.28	Gulf Penas, Patagonia region, Chile
Summer	-73.51	-44.70	Moradela Channel, Aysén Province, Chile

Season	Longitude	Latitude	Locality
Summer	-74.61	-51.51	Diego de Almagro Islands, Magellan and the Chilean Antarctic Region, Chile
Summer	-67.50	-56.50	Cape Horn, Magellan and the Chilean Antarctic Region, Chile
Summer	-74.02	-51.48	Sarmiento channel, Magellan and the Chilean Antarctic Region, Chile
Summer	-67.19	-55.98	Cape Horn, Magellan and the Chilean Antarctic Region, Chile
Summer	-74.10	-52.78	Manuela Island, Magellan and the Chilean Antarctic Region, Chile
Summer	-74.79	-44.21	Aysén region, Chile
Summer	-67.25	-55.97	Cape Horn, Magellan and the Chilean Antarctic Region, Chile
Summer	-70.07	-52.57	San Gregorio, Magellan and the Chilean Antarctic Region, Chile
Summer	-74.94	-47.51	Gulf Penas, Patagonia region, Chile
Summer	-70.82	-54.29	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Summer	-73.56	-45.22	Near to Cinco hermanas Island, Aysén region, Chile
Summer	-74.75	-47.71	Messier channel, Aysén region, Chile
Summer	-73.55	-44.85	Moralada Channel, Magellan and the Chilean Antarctic Region, Chile
Summer	-73.25	-42.42	Meulin, Chinchao, Los Lagos region, Chile
Summer	-67.15	-55.51	Cape Horn, Magellan and the Chilean Antarctic Region, Chile
Summer	-73.36	-37.22	Arauco Beach, Arauco Province, Biobío region, Chile
Summer	-68.29	-54.84	Seno de Reloncavi, Los Lagos region, Chile
Summer	-71.60	-32.77	Seno de Reloncavi, Valparaiso Province, Chile
Summer	-66.42	-55.38	Cape Horn, Magellan and the Chilean Antarctic Region, Chile
Summer	-72.90	-41.60	Seno de Reloncavi, Los Lagos region, Chile
Summer	-70.71	-53.20	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Summer	-73.72	-39.91	Punta Falsa, Valdivia Province, Chile
Summer	-67.21	-55.95	Cape Horn, Magellan and the Chilean Antarctic Region, Chile
Summer	-66.40	-55.17	Nueva Island, Magellan and the Chilean Antarctic Region, Chile
Summer	-70.61	-53.13	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile

Season	Longitude	Latitude	Locality
Summer	-74.40	-42.40	Chiloé National Park, Los Lagos region, Chile Beagle channel, near to Picton Island, Magellan and the Chilean
Summer	-66.90	-54.99	Antarctic Region, Chile Inocentes Island, Magellan and the Chilean Antarctic Region,
Summer	-74.92	-50.48	Chile
Summer	-73.52	-42.67	Detif, Puqueldon, Los Lagos region, Chile At sea near to Contreras Island, Magellan and the Chilean
Summer	-75.53	-52.20	Antarctic Region, Chile
Summer	-73.34	-41.88	Chacao Channel, Los Lagos region, Chile Near to Cape Horn, Magellan and the Chilean Antarctic Region,
Summer	-66.27	-55.78	Chile Sharpes passage, Magellan and the Chilean Antarctic Region,
Summer	-74.26	-51.28	Chile At sea near to Carlos Island, Magellan and the Chilean Antarctic
Summer	-73.83	-54.28	Region, Chile Pia Glacier, Beagle channel, Magellan and the Chilean Antarctic
Summer	-69.67	-54.84	Region, Chile Garibaldi channel, Magellan and the Chilean Antarctic Region,
Summer	-69.92	-54.84	Chile Magdalena Island, Strait of Magellan, Magellan and the Chilean
Summer	-70.66	-52.95	Antarctic Region, Chile Near to Gilbert Island, Magellan and the Chilean Antarctic
Summer	-71.17	-55.09	Region, Chile Strait of Magellan, Magellan and the Chilean Antarctic Region,
Summer	-70.72	-53.27	Chile
Summer	-73.36	-37.11	Gulf Arauco, Arauco Province, Biobío region, Chile
Summer	-67.11	-54.98	Picton Island, Beagle Channel, Chile
Summer	-73.75	-41.64	Port Godoy, Los Lagos region, Chile Seno Otway, Punta Arenas, Magellan and the Chilean Antarctic
Summer	-71.18	-52.94	Region, Chile
Summer	-65.32	-55.48	Drake Passage and nearing Beagle Channel, Chile
Summer	-73.67	-41.60	Panga point, Maullin departament, Llanquihue Province, Chile

Season	Longitude	Latitude	Locality
Summer	-60.54	-51.29	Near to Carcass Island, Malvinas/ Falkland Islands
Summer	-60.94	-51.66	West of Passage Islands, Malvinas/Falklands Islands
Summer	-57.74	-51.66	Port William, Stanley, Malvinas/Falklands Islands
Summer	-59.52	-51.80	West Falkland, Malvinas/Falkland Islands
Summer	-60.68	-51.33	Westpoint Island Malvinas/ Falklands Islands
Summer	-59.66	-52.36	Barren Island, Malvinas/Falklands Island
Summer	-59.01	-52.34	At sea near to Bleaker Island, Malvinas/Falklands Islands
Summer	-61.07	-51.59	Near to Nuevo Island, Malvinas/Falkland Islands
Summer	-60.39	-51.24	Soundeers Island, Malvinas/ Falkland Islands
Summer	-60.33	-51.29	Soundeers Island, Malvinas/ Falkland Islands
Summer	-59.37	-51.68	Port Howard, Malvinas/Falklands Islands
Summer	-58.96	-51.25	Dolphin point, Malvinas/Falklands Islands
Summer	-60.12	-51.16	Northwest Malvinas/Falkland Islands
Summer	-64.57	-42.74	Gulf Nuevo, Chubut Province, Argentina
Summer	-64.91	-42.75	Gulf Nuevo, Near to Puerto Madryn, Chubut Province, Argentina
Summer	-64.93	-42.76	Gulf Nuevo, Near to Puerto Madryn, Chubut Province, Argentina
Summer	-57.50	-37.85	Santa Clara del Mar, Buenos Aires Province, Argentina
Summer	-56.88	-38.25	Mar del Plata, Buenos Aires Province, Argentina
Summer	-57.08	-38.36	Mar del Plata, Buenos Aires Province, Argentina
Summer	-58.79	-38.61	Necochea, Buenos Aires Province, Argentina
Summer	-64.94	-40.76	San Antonio Oeste Bay, Rio Negro Province, Argentina
Summer	-64.99	-40.76	San Antonio Oeste Bay, Rio Negro Province, Argentina
Summer	-68.18	-54.85	Ushuaia Bay, near to Los Lobos Island Beagle Channel, Argentina
Summer	-64.31	-42.58	Valdés Peninsula, Punta Norte, Chubut Province, Argentina
Summer	-64.30	-42.59	Valdés Peninsula, Punta Norte, Chubut Province, Argentina
Summer	-64.88	-42.77	Puerto Madryn, Chubut Province, Argentina
Summer	-64.99	-42.78	Puerto Madryn, Chubut Province, Argentina
Summer	-64.48	-42.95	Pedral Ranch, Port Madryn, Chubut Province, Argentina
Summer	-65.50	-44.63	Punta Fabian, Camarones Bay, Chubut Province, Argentina

Season	Longitude	Latitude	Locality
Summer	-65.70	-44.80	Camarones Bay, Chubut Province, Argentina
Summer	-66.35	-45.06	Near to Ezquerra Island, Chubut Province, Argentina Tovita Island, Austral Patagonia Coastal Marine
Summer	-65.95	-45.12	Interjurisdictional Park, Argentina
Summer	-66.49	-45.18	Near to Vernaci Este Island, Chubut Province, Argentina
Summer	-66.40	-45.19	Near to Viano Mayor Island, Chubut Province, Argentina
Summer	-63.68	-45.49	Near to Gulf San Jorge, Chubut Province, Argentina
Summer	-67.62	-46.10	Caleta Olivia, Gulf San Jorge, Santa Cruz Province, Argentina
Summer	-66.15	-47.08	Mount Loayza, Santa Cruz Province, Argentina
Summer	-67.00	-54.94	Beagle Channel, Argentina Pinguino Island, Puerto Deseado, Santa Cruz Province,
Summer	-65.72	-47.90	Argentina
Summer	-67.05	-49.62	San Julian Bay, Santa Cruz Province, Argentina
Summer	-68.95	-51.63	Punta Loyola, Marjory Glen, Santa Cruz Province, Argentina
Summer	-68.36	-52.34	Cape Virgenes natural reserve, Santa Cruz Province, Argentina
Summer	-68.47	-52.52	Mouth of Strait of Magellan, Argentina
Summer	-64.53	-52.58	Atlantic Ocean, Argentina
Summer	-68.24	-52.61	Mouth of Strait of Magellan, Argentina
Summer	-67.73	-53.75	Rio Grande, Tierra del Fuego Province, Argentina
Summer	-67.70	-53.77	Rio Grande, Tierra del Fuego Province, Argentina
Summer	-66.00	-53.95	Cape San Pablo, Ushuaia Department, Argentina Observatorio Island, Tierra del fuego Province, Antarctica and
Summer	-64.21	-54.33	Atlantic south Islands Province, Argentina
Summer	-68.24	-54.88	H Island Ushuaia, Argentina
Summer	-68.35	-54.84	Ushuaia Bay, Tierra del Fuego Province, Argentina
Summer	-68.07	-54.87	Beagle Channel, Ushuaia, Argentina
Summer	-67.73	-54.90	Beagle Channel, Ushuaia, Argentina
Summer	-65.23	-54.92	Ushuaia, Tierra del Fuego Province, Argentina
Summer	-67.05	-54.93	Beagle Channel, Ushuaia, Argentina
Summer	-66.87	-54.98	Beagle Channel, Ushuaia, Argentina
Summer	-66.83	-54.98	Beagle Channel, Ushuaia, Argentina
Summer	-66.77	-55.01	Beagle Channel, Ushuaia, Argentina

Season	Longitude	Latitude	Locality
Summer	-66.30	-55.01	Slogget Bay, Ushuaia, Argentina
Summer	-65.76	-55.03	Mouth of Beagle Channel, Ushuaia, Argentina
Summer	-65.86	-55.03	Slogget Bay, Ushuaia, Argentina
Summer	-66.71	-55.04	Mouth of Beagle Channel, Ushuaia, Argentina
Summer	-66.61	-55.08	Mouth of Beagle Channel, Ushuaia, Argentina
Summer	-66.60	-55.09	Mouth of Beagle Channel, Ushuaia, Argentina
Summer	-66.55	-55.10	Mouth of Beagle Channel, Ushuaia, Argentina
Summer	-66.52	-55.10	Mouth of Beagle Channel, Ushuaia, Argentina
Summer	-65.19	-44.04	Punta Tombo, Chubut Province, Argentina
Summer	-67.58	-46.33	Puerto Deseado, Santa Cruz Province, Argentina
Summer	-65.78	-47.93	Oso Bay, Santa Cruz Province, Argentina
Summer	-57.35	-34.8	De la Plata River, Buenos Aires Province, Argentina
Summer	-53.78	-34.41	Cape Polonio, Rocha Department, Uruguay
Summer	-54.28	-34.68	Rocha Lagoon, Rocha Department, Uruguay
Summer	-50.12	-29.98	Imbé Channel, Tramandai, Rio Grande do Sul State, Brazil
Summer	-43.16	-22.96	Leme Fort, Rio de Janeiro State, Brazil
Fall	-81.01	-2.19	La Chocolatera, Salinas, Santa Elena Province, Ecuador
Fall	-81.00	-2.20	La Lobeira , Salinas, Ecuador
Fall	-77.84	-12.15	Near to Hormigas de Afuera Islands, Callao Province, Peru
Fall	-76.38	-16.01	Nazca Province, Ica Department, Peru
Fall	-77.44	-11.85	At sea near to Santa Rosa District, Lima Province, Peru
Fall	-75.50	-15.48	At sea near to Marcona District, Nazca Province, Peru
Fall	-72.10	-17.55	Near to Mollendo, Mollendo District, Arequipa region, Peru
Fall	-77.33	-12.08	Near to San Lorenzo Island, Callao region, Peru
Fall	-77.12	-12.85	Asia district, Lima Department, Peru
Fall	-77.04	-12.73	Near to Tres Islas Beach, Chilca District, Peru
Fall	-79.92	-6.88	Santa Rosa, Lambayeque region, Peru
Fall	-77.23	-12.13	Palomino Island, Callao Province, Peru
Fall	-77.17	-11.74	Ancon, Lima Department, Peru
Fall	-71.60	-33.04	Paseo Wheelwright, Valparaiso region, Chile
Fall	-73.51	-37.03	Santa Marta Island, Concepción Province, Chile
Fall	-70.42	-23.70	Antofagasta, Antofagasta Province, Chile

Season	Longitude	Latitude	Locality
Fall	-72.14	-34.83	Infiernillo Beach, Pichilemu, Cardenal Caro Province, Chile
Fall	-71.56	-30.11	Lengua de Vaca, Coquimbo region, Chile
Fall	-70.63	-53.25	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Fall	-70.68	-53.23	Punta Arenas, Magellan and the Chilean Antarctic Region, Chile
Fall	-71.95	-33.00	Valparaiso region, Chile
Fall	-73.94	-38.29	At sea near to Mocha Island Natural Reserve, Biobío region, Chile
Fall	-71.70	-33.43	Punta de Tralca, Valparaiso region, Chile
Fall	-70.47	-23.05	Mejillones Bay, Antofasta Province, Chile
Fall	-71.70	-32.95	Valparaiso region, Chile
Fall	-71.77	-33.56	San Antonio Province, Chile
Fall	-71.49	-30.25	Mouth of Estero Tongoy, Coquimbo region, Chile
Fall	-72.42	-35.31	Near to the Constitución, Talca Province, Maule region, Chile
Fall	-71.36	-29.98	La herradura Beach, Coquimbo region, Chile
Fall	-73.09	-36.61	Near to Quiriguina I, Talcahuano Province, Biobío region, Chile
Fall	-71.52	-32.76	Near to Seno de Reloncavi, Valparaiso region, Chile
Fall	-70.70	-53.28	Porvenir, Tierra del Fuego Province, Chile
Fall	-71.58	-32.77	Seno de Reloncavi, Valparaiso region, Chile
Fall	-70.67	-22.86	Mejillones Bay, Antofasta Province, Chile
Fall	-73.38	-44.23	Moraleda Channel, Aysén region, Chile
Fall	-70.67	-22.90	At sea near to Antofasta, Antofasta region, Chile
Fall	-71.63	-33.62	Mouth of Maipo River, Valparaiso region, Chile
Fall	-72.63	-35.84	Curanipe River, Cauquenes Province, Maule region, Chile
Fall	-70.21	-20.81	Punta Patache, Iquique Province, Tarapacá region, Chile
Fall	-71.52	-29.26	Punta de Choros, Damas Island, Coquimbo region, Chile
Fall	-71.64	-30.27	Caleta de Togoy, Coquimbo region, Chile
Fall	-71.53	-30.29	Togoy, Coquimbo region, Chile
Fall	-66.66	-55.06	Beagle Channel, Chile
Fall	-73.25	-41.83	Golf of Ancud, Los Lagos region, Chile
Fall	-72.90	-41.60	Seno de Reloncavi, Los Lagos region, Chile
Fall	-73.59	-43.56	Gulf of Corcovado, Los Lagos region, Chile

Season	Longitude	Latitude	Locality
Fall	-73.72	-39.91	Chaihuin, Valdivia Province, Los Ríos region, Chile
Fall	-72.00	-32.95	Valparaiso region, Chile
Fall	-73.17	-36.67	Talcahuano, San vicente, Concepción Province, Biobío region, Chile
Fall	-70.39	-23.62	Las Rocas Beach, Antofasta region, Chile
Fall	-71.64	-33.02	Valparaiso region, Chile
Fall	-71.71	-33.75	El Yali natural reserve, Valparaiso region, Chile
Fall	-70.72	-53.27	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Fall	-73.86	-41.83	Ancud, Los Lagos region, Chile
Fall	-57.75	-51.26	Malvinas/ Falkland Islands
Fall	-56.88	-38.25	Mar del Plata, Buenos Aires Province, Argentina
Fall	-58.98	-38.67	Punta Florida Beach, Buenos Aires Province, Argentina
Fall	-59.85	-38.84	Near to Balneario Orense, Buenos Aires Province, Argentina
Fall	-68.36	-52.34	Cape Virgenes Natural Reserve, Santa Cruz Province, Argentina
Fall	-66.52	-45.16	Bustamante Bay, Port Piojo, Buenos Aires Province, Argentina
Fall	-64.93	-42.75	Near to Puerto Madryn, Chubut Province, Argentina
Fall	-64.72	-42.78	Gulf Nuevo, Chubut Province, Argentina
Fall	-64.62	-42.81	Near to Puerto Madryn, Chubut Province, Argentina
Fall	-57.22	-38.11	Mar del Plata, Buenos Aires Province, Argentina
Fall	-57.08	-38.36	Mar del Plata, Buenos Aires Province, Argentina
Fall	-65.72	-47.91	Pingiüino Island, Puerto Deseado, Santa Cruz Province, Argentina
Fall	-65.19	-44.06	Punta Tombo, Chubut Province, Argentina
Fall	-66.53	-45.11	Bustamante Bay, Buenos Aires Province, Argentina
Fall	-56.61	-38.16	Mar de Plata, Buenos Aires Province, Argentina
Fall	-65.00	-42.78	Puerto Madryn, Chubut Province, Argentina
Fall	-57.74	-39.16	Necochea, Buenos Aires Province, Argentina
Fall	-53.79	-34.34	Barra de Valizas, Rocha Department, Uruguay
Fall	-54.28	-34.68	Barra de la Laguna de Rocha, Rocha Department, Uruguay
Fall	-54.94	-34.96	Virgen de Candelaria rocks, El Emir Beach, Punta del este, Uruguay

Season	Longitude	Latitude	Locality
Fall	-55.95	-34.84	Solymar, De la costa city, Montevideo Department, Uruguay Mouth of Carrasco stream, Ciudad de la Costa, Canelones
Fall	-56.02	-34.88	Department, Uruguay
Fall	-54.91	-34.94	Chiverta Beach, Punta del Este, Uruguay
Fall	-54.96	-34.97	Roquedal, Punta del Este, Uruguay
Fall	-54.90	-35.03	Lobos Island, Maldonado Department, Uruguay
Fall	-53.79	-34.40	Cape Polonio, Rocha Department, Uruguay
Fall	-56.16	-34.93	Montevideo, Montevideo Department, Uruguay
Fall	-48.49	-27.68	Campeche Beach, Florianópolis, Santa Catarina State, Brazil
Fall	-48.45	-27.63	Joaquina Beach, Florianópolis, Santa Catarina State, Brazil
Fall	-38.70	-17.97	Abrolhos National Park, Bahia State, Brazil
Fall	-41.87	-22.74	João Fernandinho Beach, Búzios, Rio de Janeiro State, Brazil
Fall	-45.16	-23.91	Ilhabela, São Paulo State, Brazil
Fall	-45.29	-23.73	Ilhabela, São Paulo State, Brazil
Fall	-44.70	-23.34	Ipanema Beach, Rio de Janeiro State, Brazil
Fall	-46.68	-24.49	Ithanhaém, São Paulo State, Brazil
Fall	-42.01	-22.98	Arraial do Cabo, Rio de Janeiro State, Brazil
Fall	-41.89	-22.76	Armação Beach, Búzios, Rio de Janeiro State, Brazil
Fall	-48.37	-27.46	Santinho Beach, Florianópolis, Santa Catarina State, Brazil
Fall	-40.29	-20.30	Vitória, Espírito Santo State, Brazil
Fall	-45.08	-23.64	Ubatuba, São Paulo State, Brazil
Fall	-45.02	-23.46	Ponta Grossa, São Paulo State, Brazil
Fall	-46.26	-24.08	Guarujá, São Paulo State, Brazil
Winter	-81.32	-2.29	Salinas, Santa Elena Province, Ecuador
Winter	-80.98	-2.20	Santa Elena Peninsula, Salinas, Santa Elena Province, Ecuador
Winter	-81.01	-2.19	La Chocolatera, Salinas, Santa Elena Province, Ecuador
Winter	-80.85	-1.59	Salango Harbor, Manabí Province, Ecuador
Winter	-80.96	-1.42	Port Lopez, Manabí Province, Ecuador
Winter	-71.22	-17.76	El Palo Beach, Moquegua Province, Peru
Winter	-71.38	-17.70	Punta Coles National Park, Peru
Winter	-72.22	-17.10	Port Faro, Peru
Winter	-76.16	-14.32	Santa Rosa Island, Peru

Season	Longitude	Latitude	Locality
Winter	-76.34	-13.92	La Mina Beach, Paracas Natural Reserve, Peru
Winter	-76.46	-13.85	Sangayan Island, Paracas Natural Reserve, Peru
Winter	-76.54	-13.74	Ballestas Island, Paracas Natural Reserve, Peru
Winter	-76.40	-13.74	Ballestas Island, Paracas Natural Reserve, Peru
Winter	-76.22	-13.71	San Andres Beach, Pisco, Peru
Winter	-76.80	-12.48	Puscana coast, Lima Department, Peru
Winter	-76.98	-12.23	Coast of south Lima, Lima Department, Peru
Winter	-77.84	-12.15	Near to Lima, Peru
Winter	-77.73	-12.11	Lima, Lima Department, Peru
Winter	-77.27	-12.10	San Lorenzo Island, Callao Province, Peru
Winter	-77.17	-12.07	La Punta district, Callao Province, Peru
Winter	-70.66	-53.26	Strait of Magellan, Magellan and the Chilean Antarctic Region, Chile
Winter	-70.68	-53.23	Porvenir, Tierra del Fuego Province, Chile
Winter	-73.48	-42.90	Queilén, Chiloé Province, Chile
Winter	-73.69	-41.78	Chacao Channel, Los Lagos region, Chile
Winter	-73.41	-39.82	Punta Loncoyén, Valdivia Province, Chile
Winter	-73.29	-39.36	Queule, Cautin Province, Araucania region, Chile
Winter	-73.34	-38.94	Puaucho Beach, Araucanía region, Chile
Winter	-73.42	-38.76	Mouth of Imperial River, Araucanía region, Chile
Winter	-58.79	-38.61	Near to camping Suteba, Necochea, Buenos Aires Province, Chile
Winter	-73.91	-38.36	Mocha Island Natural Reserve, Arauco Province, Biobío region, Chile
Winter	-73.70	-38.33	Mocha Island Natural Reserve, Arauco Province, Biobío region, Chile
Winter	-73.59	-37.15	Punta lavapié, Gulf of Arauco, Biobío region, Chile
Winter	-73.36	-37.11	Gulf of Arauco, Biobío region, Chile
Winter	-73.29	-37.09	Arauco Province, Biobío region, Chile
Winter	-73.15	-36.86	Beach in Concepción, Concepción Province, Biobío region, Chile
Winter	-73.16	-36.81	Mouth of the Biobío River, Hualpén, Biobío region, Chile

Season	Longitude	Latitude	Locality
Winter	-72.21	-35.12	Mouth of Huenchullami River, Maule region, Chile
Winter	-72.09	-34.75	Lilco, Curicó Province, Maule region, Chile
Winter	-71.63	-33.62	Maipo River, Valparaiso region, Chile
Winter	-71.77	-33.56	San Antonio Province, Chile
Winter	-71.73	-33.36	Algorrobo, Valparaiso region, Chile
Winter	-71.61	-33.04	Valparaiso, Valparaiso region, Chile
Winter	-71.90	-33.01	Humboldt current, Valparaiso region, Chile
Winter	-71.95	-33.00	Valparaiso, Valparaiso region, Chile
Winter	-72.07	-32.98	Valparaiso, Valparaiso region, Chile
Winter	-71.69	-32.93	Humboldt Current, Valparaiso region, Chile
Winter	-71.54	-32.78	Seno de Reloncavi, Valparaiso region, Chile
Winter	-71.58	-32.77	Seno de Reloncavi, Valparaiso region, Chile
Winter	-71.49	-30.25	Mouth of Estero Tongoy, Coquimbo region, Chile
Winter	-71.44	-30.18	Guanaqueros, Elqui Province, Coquimbo region, Chile
Winter	-71.38	-30.07	Totalillo, Coquimbo region, Chile
Winter	-71.36	-29.95	Emisario, Coquimbo region, Chile
Winter	-71.30	-29.93	Coquimbo bay, Coquimbo region, Chile
Winter	-71.30	-29.90	Emisario de la Serena, Coquimbo region, Chile
Winter	-71.54	-29.27	Los Choros Island, Pingüino de Humboldt National Reserve, Chile
Winter	-71.53	-29.24	Near to Dama Island National Reserve, Chile
Winter	-70.67	-26.15	El Soldado Beach, Pan de Azúcar National Park, Chile
Winter	-70.58	-25.37	Taltal, Antofasta Province, Chile
Winter	-70.79	-25.21	Taltal, 20 km offshore, Antofasta Province, Chile
Winter	-70.30	-22.86	Hornitos, Antofasta region, Chile
Winter	-70.46	-18.47	Near to Arica, Arica and Panicota region, Chile
Winter	-59.10	-52.43	Sea Lion Island, Malvinas/Falkland Islands
Winter	-68.42	-52.39	Cape Virgenes, Santa Cruz Province, Argentina
Winter	-68.36	-52.34	Cape Virgenes, Santa Cruz Province, Argentina
Winter	-64.31	-42.58	Punta Pirámides, Valdés Peninsula, Patagonia region, Argentina
Winter	-63.81	-42.07	Gulf San Matias, Chubut Province, Argentina
Winter	-61.46	-39.25	Blanca Bay, Buenos Aires Province, Argentina

Season	Longitude	Latitude	Locality
Winter	-57.74	-39.16	Necochea, Buenos Aires Province, Argentina
Winter	-59.70	-38.80	Tres arroyos, Buenos Aires Province, Argentina
Winter	-59.41	-38.76	Camping San Cayetano, Buenos Aires Province, Argentina
Winter	-58.98	-38.67	Punta Florida, Buenos Aires Province, Argentina
Winter	-58.87	-38.64	Necochea, Buenos Aires Province, Argentina
Winter	-58.88	-38.63	Punta Negra Beach, Argentina
Winter	-58.72	-38.62	Near to Necochea, Buenos Aires Province, Argentina
Winter	-57.54	-38.30	Mar de Plata, Buenos Aires Province, Argentina
Winter	-56.88	-38.25	Mar de Plata, Buenos Aires Province, Argentina
Winter	-57.32	-38.18	Mar de Plata, Buenos Aires Province, Argentina
Winter	-57.22	-38.11	Mar de Plata, Buenos Aires Province, Argentina
Winter	-57.28	-38.05	Mar de Plata, Buenos Aires Province, Argentina
Winter	-57.54	-38.00	Mar de Plata, Buenos Aires Province, Argentina
			Punta del Este, 19 nautical miles south, Maldonado Department,
Winter	-54.89	-35.26	Uruguay
Winter	-54.94	-35.11	Punta del Este, Maldonado Department, Uruguay
			Punta del Este, 20km offshore, Maldonado Department,
Winter	-54.92	-35.07	Uruguay
Winter	-54.90	-35.02	Near to Los Lobos Island, Maldonado Department, Uruguay
			Punta del este, near to Los Lobos Island Maldonado Department,
Winter	-54.93	-35.02	Uruguay
Winter	-54.97	-34.95	Gorroti Island, Murallón, Maldonado Department, Uruguay
Winter	-56.16	-34.93	Punta Carretas lighthouse, Montevideo Department, Uruguay
			Mouth of Carrasco stream, De la Costa city, Montevideo
Winter	-56.02	-34.88	Department, Uruguay
Winter	-54.64	-34.85	José Ignacio Lighthouse, Maldonado Department, Uruguay
Winter	-54.28	-34.68	Rocha Lagoon, Rocha Department, Uruguay
Winter	-54.12	-34.65	La Paloma, Rocha Department, Uruguay
Winter	-53.78	-34.41	Cape Polonio, Rocha Department, Uruguay
Winter	-53.45	-33.81	La Coronilla, Barra del Chuy, Rocha Department, Uruguay
			Beach 5 km Norte of Hermenegildo, Rio Grande do Sul State,
Winter	-53.28	-33.68	Brazil

Season	Longitude	Latitude	Locality
Winter	-50.78	-31.13	Mostradas, Rio Grande do Sul State, Brazil
Winter	-48.75	-28.49	Molhes, Santa Catarina State, Brazil
Winter	-48.35	-27.35	Arvoredo Island, Santa Catarina State, Brazil
Winter	-48.23	-25.47	Lagoa Beach, Superagui National Park, Parana State, Brazil
Winter	-46.68	-24.49	Queimada Grande Island Park, São Paulo State, Brazil
Winter	-46.80	-24.46	Queimada Grande Island Park, São Paulo State, Brazil
Winter	-46.78	-24.45	Near to Ilha das Cobras, São Paulo State, Brazil
Winter	-45.34	-23.97	Ilhabela, São Paulo State, Brazil
Winter	-45.18	-23.87	Sumitica Island, Ponta do Boi, São Paulo State, Brazil
Winter	-43.38	-23.01	Tijuca Beach, Rio de Janeiro State, Brazil
Winter	-42.01	-22.89	São Mateus Fort, Rio de Janeiro State, Brazil
Winter	-41.87	-22.74	Búzios, Rio de Janeiro State, Brazil
Winter	-40.29	-20.30	Vitória, Espírito Santo State, Brazil
Winter	-38.71	-17.97	Siriba Beach, Abrolhos, Abrolhos National Park, Brazil

Table S2. Description of the Ecological niche models for the South America Tern *Sterna hirundinacea* performed in this study following the ODMAP (Overview, Data, Model, Assessment, and Prediction) protocol (Zurell et al., 2020).

ODMAP section	ODMAP subsection	ODMAP elements
Overview	Authorship	<ul style="list-style-type: none"> • Authors: Roxiris A. Azuaje-Rodríguez, Sofia Marques Silva and Caio J. Carlos. • Contact email: roxiris6@gmail.com • Title: Not going with the flow: Ecological niche of a migratory seabird, the South American Tern <i>Sterna hirundinacea</i>. • DOI: doi:10.1016/j.ecolmodel.2021.109804
	Model objective	<ul style="list-style-type: none"> • SDM objective/purpose: Mapping and transfer • Main target output: Continuous occurrence probabilities.
	Taxon	<ul style="list-style-type: none"> • Focal taxon: South American Tern, <i>Sterna hirundinacea</i>, Laridae, Charadriiformes, Aves.
	Location	<ul style="list-style-type: none"> • Location of study area: Atlantic and Pacific coasts of South America.
	Scale of analysis	<ul style="list-style-type: none"> • Spatial Extent (Lon / Lat): Atlantic coast (longitude from -69.4°W to -33.3°E and latitude from -9.8°N to -58.6°S) and Pacific coast (longitude from -84.2°W to -67.1°E and latitude from -0.14°N to -58.01°S). • Spatial resolution: 4 km. • Temporal extent/time period: Southern Hemisphere, meteorological seasons. Time period: 1907-2019. • Type of extent boundary (e.g., rectangular, natural, political): Species distribution range and South American coastal Provinces (Fig. 1; Spalding et al. 2007).

ODMAP section	ODMAP subsection	ODMAP elements
	Biodiversity data overview	<ul style="list-style-type: none"> • Observation type (e.g., standardized monitoring data, field survey, range map, citizen science, GPS tracking, camera traps): online repositories with data derived from preserved specimens, citizen science and monitoring data. • Response/data type: Presence-only.
	Type of predictors	<ul style="list-style-type: none"> • Climatic: Seasonal variables for absorption due to phytoplankton at 443nm, chlorophyll-a concentration, photosynthetically available radiation, particulate organic carbon, particulate inorganic carbon, sea surface temperature, nightly sea surface temperature and diffuse attenuation coefficient.
	Conceptual model	<ul style="list-style-type: none"> • Hypotheses about species-environment relationships: Coastal habitats are influenced by different superficial marine currents, causing seasonality in marine productivity and biomass, and therefore have been divided into fairly well delimited Provinces. Thus, we hypothesize that coastal Provinces could be used as proxies to delimit distinct ecological niches and assist niche modelling procedures for seabirds. The South American Tern <i>Sterna hirundinacea</i> is a migratory seabird distributed along the Pacific and Atlantic coasts of South America, including the Malvinas/Falkland Islands, comprising most of the South American coastal Provinces. We use this tern species to test the utility of coastal Provinces delimitation in the niche modelling procedure for seabirds by estimating ENM's for seasons, to the entire species distribution range and its populations delimited by coastal Provinces. In addition, we

ODMAP section	ODMAP subsection	ODMAP elements
		<p>compared these ecological niches using environmental space tests.</p>
	<p>Assumptions</p>	<ul style="list-style-type: none"> • State critical model assumptions: We assumed that the species is in a non-equilibrium state. Each occurrence record is independent and represent new information. Relevant explanatory variables of species distributions are included and error free. There are no other extrapolation issues.
	<p>SDM algorithms</p>	<ul style="list-style-type: none"> • Model algorithms: MaxEnt algorithm. • Justification of model complexity: We tested three feature classes (l = linear, q = quadratic, p = product) in three different combinations ("lq", "lqp", "q"), and five different standardized multiplier values (0.1, 0.25, 0.5, 1, 2, 4). • ·Is model averaging/ensemble modelling used?: Not applicable.
	<p>Model workflow</p>	<ul style="list-style-type: none"> • Conceptual description of modelling steps including model fitting, assessment and prediction: We selected four environmental variables less correlated for the ENM's procedures. We used these variables to first calibrated ENMs for the entire species distribution range per season and projected ENM's from each of the putative breeding populations delimited by coastal provinces into the total species distribution range. Lastly, we compared ecological niches between breeding and non-breeding areas and seasons, through environmental space differentiation tests.
	<p>Software, codes and data</p>	<ul style="list-style-type: none"> • Specify modelling platform incl. version, key packages used: All analyses were performed using R v. 3.5.3 and the packages "modelos", "usdm", "kuenm" and "humboldt".

ODMAP section	ODMAP subsection	ODMAP elements
		<ul style="list-style-type: none"> Specify availability of codes: The code used is provided in the Appendix S1. Specify availability of data: We provided a table of the occurrence records used in this study (Table S1).
Data	Biodiversity data	<ul style="list-style-type: none"> Taxon name: South American Tern, <i>Sterna hirundinacea</i>, Laridae, Charadriiformes, Aves. Details on taxonomic reference system: We follow the taxonomy of the Handbook of the Birds of the World (Gochfeld et al., 2020). Ecological level: Species, populations Biodiversity data source: VertNet (vertnet.org, accessed January 2019), Xeno-canto (xeno-canto.org, accessed January 2019), and Global Biodiversity Information Facility (gbif.org, accessed July 2019). Sampling design: random. Sample size per taxon: 644 occurrence records. Country/region mask, if applicable: Calibration areas correspond to coastal marine areas within a 250 km buffer around the shore. Details on absence data collection: Not applicable Details on background data derivation: We created 10,000 random background points throughout the entire calibration area of coastal marine areas.
	Data partitioning	<ul style="list-style-type: none"> Selection of training data (for model fitting): We randomly selected 75% of data for training and 25% of testing. Selection of validation data (withheld from model fitting, used for estimating prediction error for model selection, model averaging or ensemble): The models were validated with the Bootstrap method.

ODMAP section	ODMAP subsection	ODMAP elements
	Predictor variables	<ul style="list-style-type: none"> • State predictor variables used: We obtained the following variables from global MODIS Aqua L3 SMI data: absorption due to phytoplankton at 443nm, chlorophyll-a concentration, photosynthetically available radiation, particulate organic carbon, particulate inorganic carbon, sea surface temperature, nightly sea surface temperature, and diffuse attenuation coefficient. • Details on data sources: Environmental variables were download from oceancolor.gsfc.nasa.gov, accessed August 2019. • Spatial resolution and spatial extent of raw data: Environmental variables were download at 4 km spatial resolution and clipped to the calibration area. • Map projection (coordinate reference system): WGS 84. • Temporal resolution and temporal extent of raw data: Environmental variables encompassed seasonal climatology mean composite and were download separately for each season. Each variable corresponded to the period between 2002 and 2019.
	Transfer data for projection	<ul style="list-style-type: none"> • Details on data sources: Environmental variables were download from oceancolor.gsfc.nasa.gov, accessed August 2019 • Spatial extent: Species distribution range and South American coastal Provinces. • Spatial resolution: 4km. • Temporal extent/time period: Species breeding seasons, fall and spring. Time period: 1907-2019 • Temporal resolution: Environmental variables encompassed seasonal climatology mean composite

ODMAP section	ODMAP subsection	ODMAP elements
		<p>and were download separately for each season. Each variable corresponded to the period between 2002 and 2019.</p> <ul style="list-style-type: none"> • Models and scenarios used: Only current scenarios were used. Projection were performed from breeding area and seasons to the entire species distribution range in the same season (Fig. 4). • Quantification of novel environmental conditions and novel environmental combinations: We used the same combination of environmental predictors from the calibration process to defined novel environments.
Model	Multicollinearity	<ul style="list-style-type: none"> • Methods for identifying and dealing with multicollinearity (Dormann, et al. 2013) or justification if multicollinearity is not explicitly dealt with: We performed a Pearson's correlation analysis, considering a correlation threshold $r < 0.70$ to select the environmental variables for the modelling procedures.
	Model settings	<ul style="list-style-type: none"> • Models settings for all selected algorithms (including default settings of specific platforms/packages, weighting of data etc.): We ran the MaxEnt algorithm in the kuenm package (Cobos et al., 2019) in R v. 3.5.3 (R Core Team, 2019). We performed 10 models replicates with bootstrap method for each area and season, allowing for a random 75% training and 25% testing data partition. We generate 10,000 random background points throughout the entire calibration area of the coastal marine areas (Phillips and Dudík, 2008; Phillips et al., 2009). In each replicate, we tested three feature classes (l = linear, q = quadratic, p = product) in three different combinations ("lq",

ODMAP section	ODMAP subsection	ODMAP elements
		<p>"lqp", "q"), and five different standardized multiplier values (0.1, 0.25, 0.5, 1, 2, 4).</p> <ul style="list-style-type: none"> • Details on relevant model settings for extrapolation beyond sample range, if applicable: Model transfer were performed under free extrapolation settings.
	Model estimates	<ul style="list-style-type: none"> • We use jack-knife to identify the importance and contribution of the variables to the ENM.
	Non-independence correction/analyses	<ul style="list-style-type: none"> • Method for addressing spatial autocorrelation in residuals: We removed duplicated records from the same grid square and divided all the 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 avoid the spatial and temporal autocorrelation in the data.
	Threshold selection	<ul style="list-style-type: none"> • Details on threshold selection: Not applicable.
Assessment	Performance statistics	<ul style="list-style-type: none"> • Performance statistics estimated on training data: To assess models significance, performance and complexity, we used the partial ROC with an omission rate of E= 5%, 50% random points (test occurrence records) and 500 bootstrap iterations (Mean > 1; P < 0.05; Peterson et al., 2008) and Akaike's Information Criterion (AICc = 0) to assess model's complexity (Muscarella et al., 2014). Significance and omission rates are calculated on models created with training data, using separate testing data subsets; model complexity is calculated on models created with the complete set of occurrences (Cobos et al., 2019).

ODMAP section	ODMAP subsection	ODMAP elements
		<ul style="list-style-type: none"> • Performance statistics estimated on test (truly independent) data, if applicable: Not applicable. There was no independent data available for testing.
	Plausibility check	<ul style="list-style-type: none"> • Response plots: Response curves were checked for complexity and plausibility. • Expert judgements: Maps of modelled predictions were checked by experts.
Prediction	Prediction output	<ul style="list-style-type: none"> • Prediction unit: Continuous occurrence probabilities. • Uncertainty in scenarios (e.g. climate models, land use models, storylines): Not applicable. • Visualization/treatment of novel environments: e.g., masking: Not applicable.

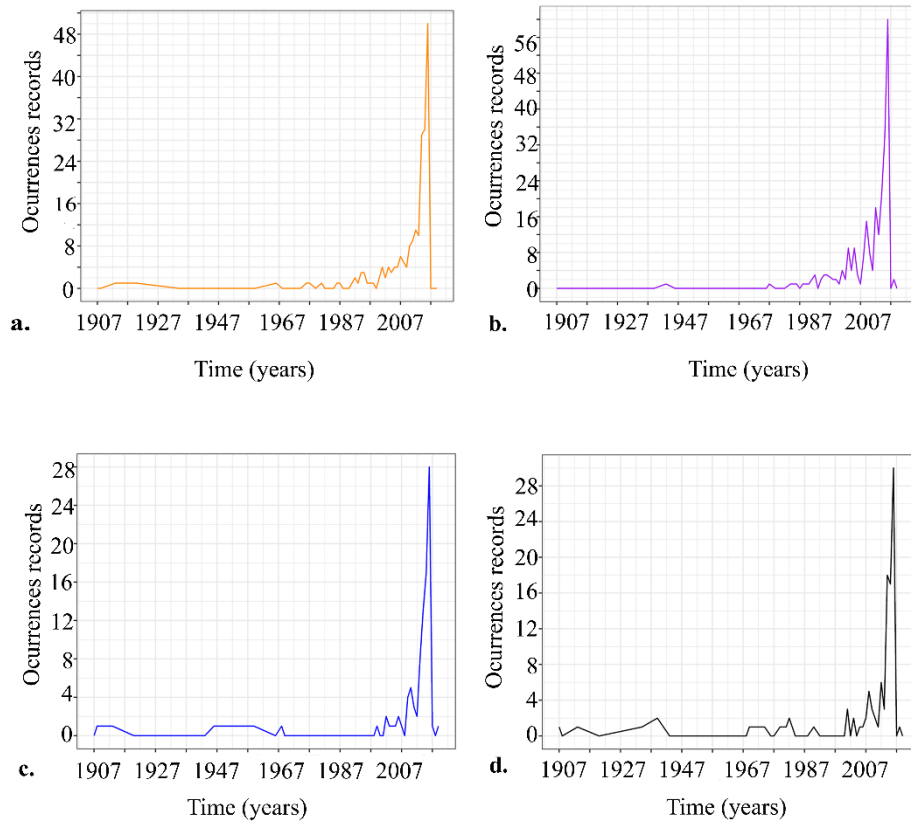


Fig. S1. Plots of the number of occurrence records, per year and season, used in the ecological niche models for the South America Tern *Sterna hirundinacea*: a. spring, b. summer, c. fall, and d. winter.

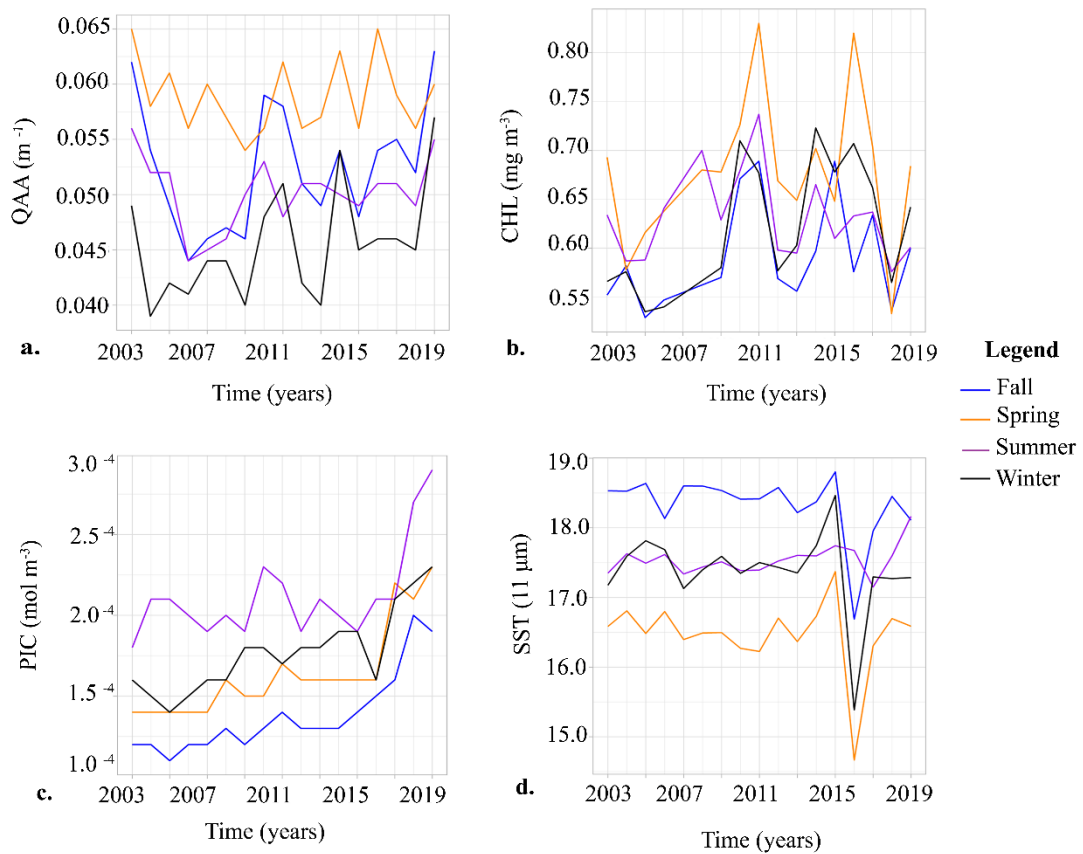


Fig. S2. Plots for the mean annual values for each environmental variable used in the ecological niche models for the South America Tern *Sterna hirundinacea*: a. absorption due to phytoplankton at 443nm (QAA), b. chlorophyll-a concentration (CHL), c. particulate inorganic carbon (PIC), d. sea surface temperature (SST).

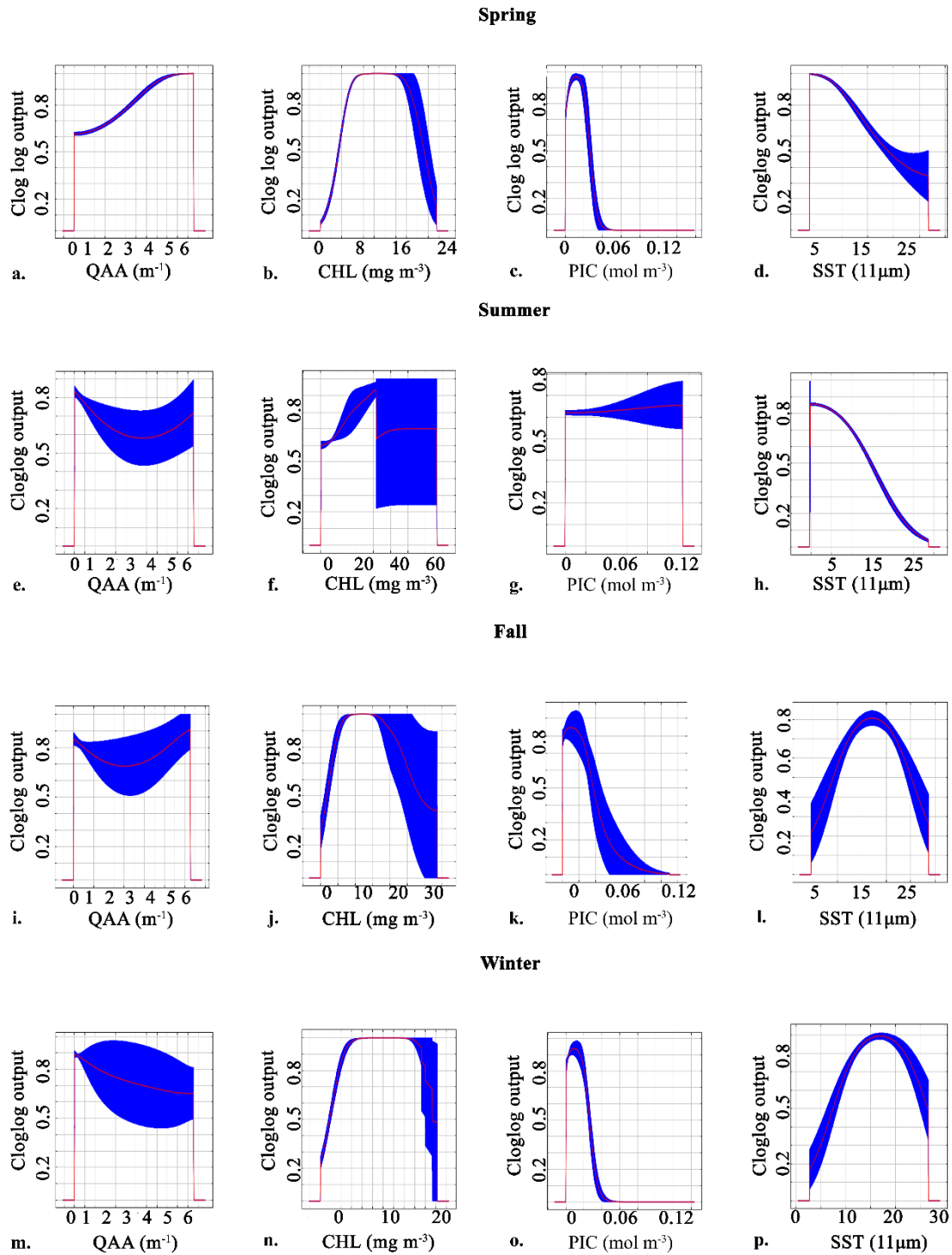


Fig. S3. Response curves for the environmental variables used in the ecological niche models of the South America Tern *Sterna hirundinacea* using Maxent. The mean response of the 10 replicates performed per model is shown, and the respective standard deviation is represented in blue. Absorption due to phytoplankton at 443nm (QAA; a., e., i., m.), Chlorophyll-a concentration (CHL; b. f., j., n.), Particulate inorganic carbon (PIC; c., g., k., o.), and sea surface temperature (SST; d., h., l., p.).

Appendix S1. R code for data preparation, occurrence records and environmental variable plots, ecological niche models and environmental comparisons performed in this study.

1. Occurrence data and environmental variable preparation

Set your working directory, and increase the memory allocated to the raster processes

```
setwd("<path to chosen working directory>")
```

```
rasterOptions(maxmemory = 1e+09)
```

Load the required libraries

```
library(sp)
```

```
library(raster)
```

```
library(modelos)
```

```
library(maptools)
```

```
library(dismo)
```

```
library(rgdal)
```

```
library(rJava)
```

```
library(rgeos)
```

```
library(MASS)
```

```
library(adehabitatMA)
```

```
library(kernlab)
```

```
library(dplyr)
```

```
library(leaflet)
```

```
library('devtools')
```

```
library(usdm)
```

Load the environmental variables


```

predictors = list.files("<path to environmental raster's>", pattern = ".tif", full.names = T)

predictors=stack(predictors)

plot(predictors)

# Load a shape file of your calibration area to cut your predictor variables

shape=readOGR("<path to the calibration area shape file>")

# and set its predictor variables CRS.

shape=spTransform(shape, CRSobj=crs(predictors))

plot(shape)

# The cut.raster function will create a new folder in your directory called "cortados" that

# will contain the variables cut with the calibration area

cut.raster(predictors, shape, dir = shape, extension = ".tif")

# Checking the new cut variables

predictors_cut = stack(list.files("cortados", pattern = ".tif", full.names = T))

plot(predictors_cut[[1]])

plot(predictors_cut[[2]])

# and so forth...

# Extract the values from the environmental variables to performed a Pearson's

# correlation analysis

valores <- values(predictors_cut)

valores[1:5,]

nrow(valores)

valores2 <- xyFromCell(predictors_cut, 1:nrow(predictors_cut))

valores2[1:5,]

nrow(valores2)

```

```

valores3 <- cbind(valores2, valores)

valores3[1:5,]

nrow(valores3)

valores3 <- na.omit(valores3)

nrow(valores3)

head(valores3)

colnames(valores3)

valores4<-(valores3[,3:10])

correlation<-cor(valores4, method="pearson")

write.csv(correlation, file="name of the file.csv")

# Select the environmental variables less correlated from the .csv file using a correlation
# threshold  $r < 0.70$  and save this selected variables in a different folder.

# Load your occurrence data

species= read.csv(file.choose(), header=TRUE, sep=",")

# Use your predictors stack to clean and filter the occurrence records

species_clean <-clean(species[, 2:3], predictors_cut)

# Save the clean occurrence records in a new .csv file

write.table(species_clean, "species_clean.csv", row.names=F, sep=",")

```

2. Occurrence records and Environmental variable plots

```

# Load the required libraries

library(gridExtra)

library(cowplot)

library(ggplot2)

```

```

# Load all the occurrence records organized by season and years in a .csv file

occurrence= read.csv(file.choose(), header=TRUE, sep=",")

# Sort the records by season and year

spring <- occurrence$Spring

summer <- occurrence$Summer

fall <- occurrence$Fall

winter <- occurrence$Winter

year <- occurrence$Year

# Make a plot for each season, for example spring

spring_plot <- ggplot() + geom_line(aes(y = spring, x = year),
                                   data = occurrence, colour= "darkorange") +
  scale_x_continuous(breaks=seq(1907,2019,10))+
  scale_y_continuous(breaks=seq(0,60,4))+
  theme(text=element_text(family="Times", face= "bold"))

spring_plot + theme_bw()

# Save the plot for each season

ggsave("spring.tiff", units="in", width=5, height=4,dpi=1000, compression = 'lzw')

# Run again the same code for the other seasons

# Now for the environmental variables, load the .csv file for the Mean annual value for
# each environmental variable

var= read.csv(file.choose(), header=TRUE, sep=",")

var_plot <- ggplot(var, aes(x = years, y = value)) + geom_line(aes(color = season)) +
  scale_color_manual (values = c("blue", "darkorange", "red", "black")) +
  scale_x_continuous(breaks=seq(2003,2019,2)) + theme_light()

```

```

var_plot + scale_y_continuous(name= "mg m-3")

# Save the plot

ggsave("name.tiff", units="in", width=5, height=4, dpi=300, compression = 'lzw')

# Run again the same code for the other variables

# Combine the variables into a single plot

mapa<-grid.arrange(aph2_plot, chl_plot, pic_plot, sst_plot)

```

3. Ecological niche models (ENM)

```

# ENM with 'kuenm' package

# Load the required libraries

library(kuenm)

library(raster)

# Set the working directory

setwd("<path to chosen working directory>")

# Load your occurrence records

occs <- read.csv("occurrence.csv")

# Split training and testing occurrence records

set.seed(1)

split <- kuenm_occsplit(occ = occs, train.proportion = 0.75, method = "random" save =
TRUE, name = "occs ")

# Prepare the sets of variables. In this case, we used only one set of variables

help(kuenm_varcomb)

vs <- kuenm_varcomb(var.dir = "Variables", out.dir = "M_variables", min.number = 4,

in.format = "ascii", out.format = "ascii")

```

```

# Models' calibration

oj <- " occs _joint.csv"

otr <- " occs _train.csv"

mvars <- "M_variables"

bcal <- "batch_cal"

candir <- "Candidate_models"

regm <- c(0.1, 0.25, 0.5, 1, 2, 4)

fclas <- c("lq", "lqp", "q")

mxpath <- "<path the Maxent java directory>"

kuenm_cal(occ.joint = oj, occ.tra = otr, M.var.dir = mvars, batch = bcal, out.dir = candir,
          max.memory = 5000, reg.mult = regm, f.clas = fclas, args= NULL,
          maxent.path =mxpath , wait = FALSE, run = TRUE)

# Evaluate candidate models

ote <- " occs _test.csv"

cresdir <- "Calibration_results"

kuenm_ceval(path = candir, occ.joint = oj, occ.tra = otr, occ.test = ote, batch = bcal,
            out.eval = cresdir, threshold = 5, rand.percent = 50, iterations = 500,
            kept = TRUE, selection = "OR_AICc", parallel.proc = FALSE)

# Model projections for the first modelling approach

bfmod <- "batch_model"

moddir <- "Final_models"

gvars <- "g_variables"

kuenm_mod(occ.joint = oj, M.var.dir = mvars, out.eval = cresdir, batch = bfmod,
          rep.n = 10, rep.type = "Bootstrap", jackknife = TRUE, out.dir = moddir,

```

```

max.memory = 1000, out.format = "cloglog", project = FALSE,
G.var.dir = gvars, ext.type = "no_ext", write.mess = FALSE,
write.clamp = FALSE, maxent.path = mxpath, args = NULL,
wait = FALSE, run = TRUE)

# For the second modelling approach, we run the above code with the options

# project = TRUE and ext.type = "ext"

# Summary of results

sname <- "species name"

modstats <- "Final_Model_Stats"

scenarios <- c("current")

kuenm_modstats(sp.name = sname, fmod.dir = moddir, format = "asc",
               project = TRUE, statistics = c("med"), replicated = TRUE,
               proj.scenarios = c("current"), ext.type = "ext", out.dir = modstats)

```

4. *Environmental space comparisons*

```

# Load required libraries

library(devtools)

library(raster)

library(humboldt)

# Set your working directory

setwd("<path to chosen working directory>")

# Load the environmental variables in a txt format

pop1 <- read.table("predictors_1.txt", h=T)

pop2 <- read.table("predictors_2.txt", h=T)

```

```

pop1<-humboldt.scrub.env(pop1)

pop2<-humboldt.scrub.env(pop2)

# Load the occurrence data

pop_1= read.csv(file.choose(), header=TRUE, sep=",")

pop_2= read.csv(file.choose(), header=TRUE, sep=",")

# Run the Niche overlap test (NOT)

full<-humboldt.doitall(inname="NOT_test", env1=pop1, env2=pop2, sp1=pop_1,
sp2=pop_2, rarefy.dist=50, rarefy.units="km", env.reso=0.041666668, reduce.env=0,
reductype="PCA", non.analogous.environments="YES",correct.env=T, env.trim=F,
env.trim.type="RADIUS", trim.buffer.sp1=250, trim.buffer.sp2=250, pcx=1, pcy=2,
col.env=e.var, e.var=c(3:6), nae.window=5, R=100, kern.smooth=0.75, e.reps=200,
b.reps=200, nae="YES",thresh.espace.z=0.0001, p.overlap=T, p.boxplot=T,
p.scatter=T,run.silent=F, color.ramp= 1, ncores=2)

# Run the Niche divergence test (NDT)

shared<-humboldt.doitall(inname="NDT_test", env1=pop1, env2=pop2, sp1=pop_1,
sp2=pop_2, rarefy.dist=50, rarefy.units="km", env.reso=0.041666668, reduce.env=2,
reductype="PCA", non.analogous.environments="NO", correct.env=T, env.trim=T,
env.trim.type="RADIUS", trim.buffer.sp1=250, trim.buffer.sp2=250, pcx=1, pcy=2,
col.env=e.var, e.var=c(3:6), R=100, kern.smooth=0.75, e.reps=200, b.reps=200,
nae="NO",nae.window=5, thresh.espace.z=0.0001, p.overlap=T, p.boxplot=T,
p.scatter=T, run.silent=F, color.ramp= 1, ncores=2)

# Run the Niche truncation index (PNTI)

# Convert the geographic space to space for measuring pnt.index

zz<-humboldt.g2e(env1=pop1, env2=pop2, sp1=pop_1, sp2=pop_2, reduce.env = 0,
reductype = "PCA", non.analogous.environments = "YES", env.trim= T, e.var=c(3:6),
col.env = e.var, trim.buffer.sp1 = 250, trim.buffer.sp2 = 250, rarefy.dist = 50,
rarefy.units="km", env.reso=0.041666668, kern.smooth = 0.75, R = 100, run.silent = F)

# Store space scores for sp1 and environments 1, 2 and both environments combined

# output from humboldt.g2e

```

```
scores.env1<-zz$scores.env1[1:2]
scores.env2<-zz$scores.env2[1:2]
scores.env12<- rbind(zz$scores.env1[1:2],zz$scores.env2[1:2])
scores.sp1<-zz$scores.sp1[1:2]
scores.sp2<-zz$scores.sp2[1:2]
pnt1<humboldt.pnt.index(scores.env12,scores.env1,scores.sp1,kern.smooth=0.75,
R=100)
pnt2<- humboldt.pnt.index(scores.env12,scores.env2,scores.sp2,kern.smooth=0.75,
R=100)
```


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CONCLUSÕES GERAIS

Nossos resultados refutaram nossas hipóteses que indicam que as províncias costeiras estão gerando estruturação ecológica, morfológica e genética nas populações do trinta-réis-de-bico-vermelho *Sterna hirundinacea*. Constatou-se que as diferenças ambientais de cada província costeira e o isolamento alocrônico entre as populações costeiras do Sul e do Norte não estão causando diferenciação e isolamento entre as populações. No entanto, nossas análises detectaram variação ambiental e regional no nicho ecológico da espécie, dimorfismo sexual e variação geográfica na morfologia entre as populações que de outra forma seriam despercebidas.

O nicho ecológico potencial do trinta-réis-de-bico-vermelho é influenciado principalmente por variáveis ambientais relacionadas a regulação dos ecossistemas marinhos como a produtividade marinha e disponibilidade de presas, do mesmo jeito como é observado para outras espécies de aves marinhas (GALL *et al.*, 2017; RIVAS, 2010; SCALES *et al.*, 2016; THIEL *et al.*, 2007; WEICHLER *et al.*, 2004). Por outro lado, a variabilidade temporal observada no nicho potencial não parece ser suficiente para causar divergência ambiental. No entanto, as populações do trinta-réis-de-bico-vermelho podem ocupar diferentes espaços ambientais durante as épocas de reprodução, particularmente nas províncias do Sudoeste Temperado Quente do Atlântico e Sudoeste Temperado Quente do Pacífico no outono. Isso provavelmente resulta de diferenças na escolha de microhabitats e áreas que podem levar à diferenciação do espaço ambiental em aves marinhas espécies (BURG; CROXAL, 2001).

Com respeito à morfologia, o trinta-réis-de-bico-vermelho apresentou dimorfismo sexual para a altura e comprimento do bico; em ambos os casos, os machos apresentaram bicos mais longos e mais grossos do que as fêmeas. O dimorfismo sexual também tem sido observado em outras espécies de trinta-réis, sendo os machos também maiores que as fêmeas em outras medidas, como comprimento da cabeça, profundidade do bico (PALESTIS *et al.*, 2012 a, b; GOCHFELD; BURGER, 2022; HATCH *et al.*, 2020; ARNOLD *et al.*, 2020). Apesar de não encontrarmos estruturação morfológica entre as populações do trinta-réis-de-bico-vermelho, observamos diferenças geográficas na largura do bico, comprimento do tarso e total da cauda entre os espécimes da província do Sudoeste Temperado Quente do Pacífico. Estas diferenças morfológicas podem ser

influenciadas tanto pela presença de alocria como por diferentes fatores ecológicos e genéticos (GRANADEIRO, 1993; MOLLER, 2001; HENDRY; DAY, 2005; BULL, 2006; LARANJEIRO *et al.*, 2022).

Finalmente, a forte conectividade migratória do trinta-réis-de-bico-vermelho contribui na manutenção do fluxo gênico e na baixa variação genética encontrada entre as populações. O possível comportamento não filopátrico, a sua alta sensibilidade a distúrbios antropogênicos e a capacidade de mudar seus locais de reprodução são considerados fatores muito importantes na formação e crescimento de novas colônias do trinta-réis-de-bico-vermelho. Por fim, a modificação dos ambientes costeiros causada pelos ciclos climáticos glaciais e interglaciais durante o Pleistoceno é considerada a principal responsável pela diversificação do clado do trinta-réis-de-bico-vermelho e outras espécies de aves marinhas (FRIESEN *et al.*, 1996; FARIA *et al.*, 2010; HILTON, 2021).

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