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DESOVA ESPORÁDICA DE TARTARUGAS MARINHAS NO SUL SUBTROPICAL DO BRASIL: SERIA ESTA REGIÃO UMA ÁREA DE DESOVA BIOCLIMATICAMENTE ADEQUADA PARA TARTARUGA-CABEÇUDA (*Caretta caretta*)?

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Dissertação 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 Mestre em Biologia Animal.

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Orientador(a): Prof. Dr. Márcio Borges Martins.

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Aprovada em ____ de _____ de _____.

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Marlene, Daniel e Socorro.

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RESUMO

Foram compiladas evidências de desova de tartarugas marinhas na costa sul do Brasil, obtidas ao longo de quase 30 anos de estudos, com estudo focado na tartaruga-cabeçuda (*Caretta caretta*). Foram comparadas áreas de nidificação na costa do Brasil e do mundo para entender a probabilidade com que a ecorregião marinha da *Southern Subtropical Shelf* (SSS) possa estar dentro da área de adequação ambiental para nidificação da espécie. Avaliou-se como o nicho bioclimático da tartaruga-cabeçuda se comporta em nível global, testando se há ou não evidências de divergência de nicho em diferentes regiões, a fim de melhor estimar a potencial adequação da SSS. Há evidências de que as áreas de desova de tartaruga-cabeçuda podem estar em desequilíbrio bioclimático, por razões comportamentais e biogeográficas. Ao mesmo tempo, já foi sugerido que as mudanças climáticas projetadas para as próximas décadas podem afetar o sucesso reprodutivo nas áreas de desova em regiões de clima tropical, mesmo com possíveis ajustes fenológicos na reprodução. Assim, é importante entender a importância que novas áreas aptas podem ter para a espécie. O Niche Equivalent Test (NOT) e o Niche Divergence Test (NDT) foram realizados utilizando a linguagem R através do pacote Humboldt, além de modelos de nicho baseados no algoritmo de máxima entropia (MAXENT). Como resultado, verificou-se que as praias de desova de tartaruga-cabeçuda ocupam apenas uma fração do nicho bioclimático disponível em áreas costeiras tropicais e subtropicais do mundo, apresentando evidências de desequilíbrio bioclimático. A *Southern Subtropical Shelf* (SSS) parece apresentar uma adequação bioclimática para desova equivalente aos valores mais baixos observados em praias regulares no Brasil, mas superiores a muitas praias ao redor do mundo.

CAPÍTULO I

Introdução geral

Introdução

Das sete espécies existentes de tartarugas marinhas, cinco delas ocorrem na costa brasileira para fins de alimentação e reprodução, sendo elas: a tartaruga-cabeçuda *Caretta caretta*, a tartaruga-verde *Chelonia mydas*, a tartaruga-de-couro *Dermochelys coriacea*, a tartaruga-de-pente *Eretmochelys imbricata* e a tartaruga-oliva *Lepidochelys olivacea* (MARCOVALDI & MARCOVALDI, 1999; ICMBIO, 2011).

As tartarugas marinhas têm ampla distribuição e são geralmente encontradas em mares tropicais e subtropicais (EPPERLY & FRAZIER, 2000). São animais migradores de longas distâncias, estabelecendo seus nichos ecológicos em diversos ambientes marinhos e regiões geográficas distintas, ao longo das diferentes fases do seu ciclo de vida, variando de ambientes pelágicos quando filhotes para diversas áreas costeiras nas fases juvenis e adultas (BOLTEN, 2003). Com exceção da desova e do desenvolvimento embrionário, que ocorrem em praias tropicais, estes animais cumprem todo seu ciclo de vida no mar (BOLTEN, 2003; GLEN & MROSOVSKY, 2004).

Mudanças climáticas induzidas por atividades antrópicas estão remodelando a biodiversidade do planeta (HOEGH-GULDBERG & BRUNO, 2010; DIFFENBAUGH & FIELD, 2013; BATLLORI *et al.*, 2017). O abuso da ação humana, combinado com a destruição de habitats naturais, causam grandes declínios na abundância da megafauna marinha, afetando as tartarugas marinhas (TROËNG & RANKIN, 2005) e outros animais, como baleias (ROMAN & PALUMBI, 2003) e tubarões pelágicos (BAUM & MYERS, 2004). Tais mudanças também afetam a distribuição, fenologia, fisiologia e comportamento de inúmeras espécies (ROOT *et al.*, 2003; PARMESAN, 2006; BELLARD *et al.*, 2012). As áreas de desova das tartarugas marinhas podem ser afetadas simultaneamente por múltiplos processos climáticos, como aumento da temperatura, elevação do nível do mar e atividade ciclônica (HAWKES *et al.*, 2009; POLOCZANSKA *et al.*, 2009). A elevação do nível do mar e a atividade ciclônica podem causar perda e/ou alteração das praias de nidificação e mortalidade de ovos (PIKE & STINER, 2007; VAN HOUTAN & BASS, 2007; FISH *et al.*, 2008; FUENTES *et al.*, 2010).

Diversos fatores ambientais determinam a adequabilidade das praias utilizadas como áreas de desova para as tartarugas marinhas e tais aspectos atuam em diferentes escalas espaciais (COLMAN *et al.*, 2020). O clima, principalmente a temperatura, tende a limitar a variedade de áreas apropriadas para a postura de ovos (PIKE, 2013). Regionalmente, condições que facilitem a migração de filhotes recém-nascidos para habitats de estuário, como áreas costeiras próximas a correntes marinhas, podem influenciar a densidade de ninhos (PUTMAN *et al.*, 2010; OKUYAMA *et al.*, 2011; SHILLINGER *et al.*, 2012; PUTMAN, 2018). Em termos de localidade, a topografia da praia exerce funções importantes na seleção da área para desova de tartarugas marinhas (PRICE *et al.*, 2018). Isso significa que alterações na iluminação, dunas de areia, vegetação, substrato e até mesmo na inclinação da praia podem lesar o comportamento das fêmeas (MAURER & JOHNSON, 2017) e consequentemente afetar o sucesso reprodutivo das espécies (FERNANDES *et al.*, 2016).

O retorno das fêmeas à terra está diretamente ligado à reprodução, pois as tartarugas marinhas enterram seus ovos sob as praias arenosas (PIKE, 2013). Ovos em incubação são extremamente sensíveis às condições hídricas e térmicas dentro do ninho e toleram apenas pequenas flutuações nessas variáveis (ACKERMAN, 1997; DAVENPORT, 1997). Após a postura dos ovos, o desenvolvimento dos embriões está sujeito à influência de fatores ambientais altamente dependentes das condições climáticas vivenciadas durante o período de incubação (MONSINJON *et al.*, 2019). Isso significa que o sucesso de eclosão e a determinação do sexo dos filhotes de tartarugas marinhas dependem intrisecamente das temperaturas de incubação.

De acordo com experimentos realizados por Howard *et al.* (2014), a eclosão ocorre dentro da faixa térmica de aproximadamente 25-35 °C. Limites mais baixos de temperatura levam à falha do desenvolvimento dos embriões e temperaturas mais altas causam a morte. Ainda no estudo de Howard *et al.* (2014), foi observado que as temperaturas dos ninhos podem ultrapassar 35 °C em algumas populações, acontecendo pouco antes da emergência dos filhotes. Mesmo acima da temperatura, os ovos eclodem com sucesso. Apesar de superar a faixa de tolerância, filhotes incubados em ninhos de temperatura mais alta podem apresentar menor sucesso de eclosão, taxa de emergência e tamanho corporal menor, maiores taxas de anormalidades morfológicas e/ou desempenho locomotor reduzido (FISHER *et al.*, 2014; CAVALLO *et al.*, 2015).

Além disso, as tartarugas marinhas possuem determinação sexual dependente do efeito cumulativo da temperatura, produzindo fêmeas em altas temperaturas de incubação e machos em baixas temperaturas de incubação (YNTEMA & MROSOVSKY, 1980; LIMPUS *et al.*, 1985; RAFFERTY *et al.*, 2017; MONTERO *et al.*, 2018). Muitas áreas de desova já produzem ninhadas predominantemente fêmeas, com algumas regiões apresentando taxas próximas de 100% (HAYS *et al.*, 2017; JENSEN *et al.*, 2018).

O aumento nas temperaturas de incubação acarreta numa defasagem da produção de machos, podendo afetar o sucesso reprodutivo a longo prazo dessas populações (FUENTES *et al.*, 2011; SANTIDRIÁN TOMILLO *et al.*, 2012; WEBER *et al.*, 2012; MONSINJON *et al.*, 2019). Os níveis atuais de temperatura provavelmente atingem ou excedem o limite superior para o desenvolvimento bem-sucedido de filhotes, pois estudos relatam baixo sucesso de incubação em diversas praias de desova (VALVERDE *et al.*, 2010; HORNE *et al.*, 2014; RAFFERTY *et al.*, 2017). Em decorrência disso, é esperado que o aquecimento de temperaturas venha a colocar a reprodução de muitas populações de tartarugas marinhas em risco.

Os primeiros estudos com tartarugas marinhas baseados na marcação de indivíduos mostraram que as fêmeas retornam às mesmas praias que nasceram para desovar (CARR & OGREN, 1960; CARR *et al.*, 1978). A filopatria está presente em muitos táxons (HUETER *et al.*, 2005; ENGELHAUPT *et al.*, 2009; RUEGER *et al.*, 2020; ELLIS *et al.*, 2021), inclusive em tartarugas marinhas. Estudos genéticos relataram que tal fidelidade ao local de desova era realmente uma filopatria, uma vez que as praias utilizadas pelas fêmeas correspondiam às áreas em que elas tinham nascido (MEYLAN *et al.*, 1990; ALLARD *et al.*, 1994; BOWEN & KARL, 2007). A filopatria em tartarugas marinhas, no entanto, não está restrita às fêmeas, sendo também observada em machos (DUTTON *et al.*, 2013; NARO-MACIEL, 2014; CLUSA *et al.*, 2018).

Filhotes recém-nascidos seriam capazes de memorizar diferentes sinais químicos e magnéticos das praias de onde eclodiram e, durante a fase adulta, usar tais informações para encontrar sua praia natal e reproduzir (LOHMANN *et al.*, 1997; LOHMANN *et al.*, 2008; LOHMANN *et al.*, 2013; LOHMANN *et al.*, 2019). Além disso, mudanças climáticas podem impactar as populações de tartarugas marinhas devido à sua determinação de sexo por temperatura (TSD) (YNTEMA & MROSOVSKY, 1980). O aquecimento global, quando

combinado com a filopatria, leva a crer num desequilíbrio nas proporções sexuais dos ninhos e na limitação da dispersão para praias mais frias como contramedida (HAWKES *et al.*, 2007; WITT *et al.*, 2010). A dificuldade em colonizar novos habitats também pode estar relacionada ao provável desequilíbrio de nicho causado pelos ciclos glaciais do Pleistoceno, onde o alcance e distribuição das espécies foram severamente alteradas (HEWITT, 2000; DALÉN *et al.*, 2007; FOOTE *et al.*, 2013). Populações dos mais variados táxons sofriam fases recorrentes de contração e isolamento durante eventos glaciais, passando por expansão populacional e contato secundário com populações anteriormente isoladas durante períodos interglaciais (HEWITT, 2000).

A espécie de tartaruga marinha com maior número de estudos é a tartaruga-cabeçuda (*C. caretta*). Ela está amplamente distribuída em águas tropicais e temperadas ao redor de todo o mundo (PRITCHARD & TREBBAU, 1984) e está listada como vulnerável pela IUCN (CASALE & TUCKER, 2017). A tartaruga-cabeçuda (*C. caretta*) é a espécie de tartaruga marinha mais abundante ao longo da costa brasileira (MARCOVALDI & MARCOVALDI, 1999). A população brasileira da espécie é uma das maiores do mundo, atrás de Marisah, Omã, e leste da Flórida, Estados Unidos da América (MARCOVALDI & CHALOUPKA, 2007). Suas principais áreas de desova no Brasil estão localizadas em Sergipe, norte da Bahia, norte do Espírito Santo e norte do Rio de Janeiro (MARCOVALDI & CHALOUPKA, 2007). Apesar da abundância e ampla distribuição das áreas de desova no sudeste e nordeste do Brasil, é provável que a distribuição atual das áreas de desova de tartaruga-cabeçuda (*C. caretta*) esteja em desequilíbrio bioclimático. A espécie é conhecida por desovar em áreas de clima subtropical e temperado ameno. As mudanças climáticas do Pleistoceno afetaram a distribuição em latitudes mais altas e a colonização posterior nessas regiões é afetada pela alta taxa de filopatria da espécie (CLUSA *et al.,* 2018).

No que diz respeito à estrutura genética de tartarugas-cabeçudas (*C. caretta*) no Brasil, estudos realizados por Reis *et al.* (2010) sugerem a existência de dois estoques genéticos: o estoque norte (viveiros Sergipe e Bahia) e o estoque sul (viveiros Espírito Santo e Rio de Janeiro). Embora as tartarugas marinhas sejam reconhecidas globalmente como um táxon ameaçado de extinção, existem ainda poucos esforços para avaliar o equilíbrio e a suscetibilidade bioclimática das áreas de desova para a tartaruga-cabeça (*C. caretta*). É necessário obter mais evidências sobre como as populações de tartaruga-cabeça (*C. caretta*)

podem ser impactadas pelas mudanças climáticas, explorando a influência de variáveis climáticas nas áreas de desova para a espécie. Isso permitirá avaliar melhor os impactos e projetar ações para sua remediação.



Fig. 1. Tartaruga-cabeçuda (*Caretta caretta*) em tanque de reabilitação no CECLIMAR/UFRGS (Foto: Márcio Borges Martins).

Objetivos

No presente estudo, foram compiladas evidências de desovas de tartarugas marinhas na costa sul do Brasil, obtidas ao longo de quase 30 anos de estudos. Dada a abundância e ocorrência comum em águas subtropicais, o estudo foi focado na tartaruga-cabeça (*C. caretta*). Foram comparadas áreas de desova presentes na costa do Brasil e do mundo para entender qual a probabilidade da ecorregião marinha *Southern Subtropical Shelf* (SSS) estar dentro da área de adequabilidade ambiental para desovas da espécie. Avaliou-se como o nicho bioclimático da tartaruga-cabeçuda (*C. caretta*) se comporta em nível global, testando se há ou não evidências de divergência de nicho em diferentes regiões, visando estimarmos melhor a adequabilidade potencial da SSS.

Existem evidências de que as áreas de desova de tartaruga-cabeçuda (*C. caretta*) possam estar em desequilíbrio bioclimático, por questões comportamentais e biogeográficas. Ao mesmo tempo, já foi sugerido que as mudanças climáticas projetadas para as próximas décadas podem afetar o sucesso reprodutivo de áreas de desova em regiões de clima tropical, mesmo com ajustes fenológicos possíveis na reprodução. Dessa forma, é importante entender qual a importância que novas áreas adequadas podem vir a ter para a espécie.

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CAPÍTULO II

Artigo:

DESOVA ESPORÁDICA DE TARTARUGAS MARINHAS NO SUL SUBTROPICAL DO BRASIL: SERIA ESTA REGIÃO UMA ÁREA DE DESOVA BIOCLIMATICAMENTE ADEQUADA PARA TARTARUGA-CABEÇUDA (*Caretta caretta*)?

Daniel Oliveira Cutrim[1,2,3], Diego Janisch Alvares[2,6], Maurício Tavares[4,5], Cariane Campos Trigo[4,5] e Márcio Borges-Martins[1,2,6]

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Sporadic nestings of sea turtles in subtropical southern Brazil: is the region a bioclimatic suitable nesting area for loggerhead sea turtles (*Caretta caretta*)?

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Abstract

In the present study, we compile evidence of nesting sea turtles on the southern coast of Brazil, obtained over almost 30 years of studies, focusing our study on the loggerhead turtle (*Caretta caretta*). We compared nesting areas on the coast of Brazil and the world to understand the probability that the Southern Subtropical Shelf (SSS) marine ecoregion is within the area of environmental suitability for nesting of the species. We evaluated how the bioclimatic niche of the loggerhead turtle behaves at a global level, testing whether or not there is evidence of niche divergence in different regions, in order to better estimate the potential suitability of SSS. There is evidence that nesting areas of loggerhead turtle may be in bioclimatic imbalance, for behavioral and biogeographic reasons. At the same time, it has already been suggested that climate changes projected for the next decades may affect the reproductive success of nesting areas in tropical climate regions, even with possible phenological adjustments in reproduction. Thus, it is important to understand the importance that new suitable areas may have for the species. The Niche Overlap Test (NOT) and Niche Divergence Test (NDT) were performed using the R with Humboldt R Package, in addition to niche models generated from MAXENT. As a result, loggerhead turtle nesting beaches were found to occupy only a fraction of the bioclimatic niche available in tropical and subtropical

coastal areas of the world, showing evidence of bioclimatic imbalance. The Southern Subtropical Shelf (SSS) seems to present a bioclimatic suitability for spawning equivalent to the lowest values observed in regular beaches in Brazil, but superior to many beaches around the world.

Keywords: Bioclimatic niche; sea turtle; loggerhead turtle; South America.

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1. Introduction

Sea turtles have a wide distribution and are generally found in tropical and subtropical seas (Epperly & Frazier, 2000). They are long-distance migratory animals, establishing their ecological niches in different marine environments and different geographic regions, throughout the different stages of their life cycle, ranging from pelagic environments when young to different coastal areas in the juvenile and adult stages (Bolten, 2003). Except for nesting and embryonic development, which occur on tropical beaches, these animals fulfill their entire life cycle at sea (Bolten, 2003; Glen & Mrosovsky, 2004).

Human-induced climate change is reshaping the planet's biodiversity (Hoegh-Guldberg & Bruno, 2010; Diffenbaugh & Field, 2013; Batllori *et al.*, 2017). The abuse of human action, combined with the destruction of natural habitats, causes large declines in the abundance of marine megafauna, affecting sea turtles (Troëng & Rankin, 2005) and other animals such as whales (Roman & Palumbi, 2003) and pelagic sharks. (Baum & Myers, 2004). Such changes also affect the distribution, phenology, physiology and behavior of numerous species (Root *et al.*, 2003; Parmesan, 2006; Bellard *et al.*, 2012). The nesting areas of sea turtles can be affected simultaneously by multiple climatic processes, such as temperature increase, sea level rise and cyclonic activity (Hawkes *et al.*, 2009; Poloczanska *et al.*, 2009). Rising sea levels and cyclonic activity can cause loss and/or alteration of nesting beaches and egg mortality (Pike & Stiner, 2007; Van Houtan & Bass, 2007; Fish *et al.*, 2008; Fuentes *et al.*, 2010).

Several environmental factors determine the suitability of beaches used as nesting grounds for sea turtles and these aspects act at different spatial scales (Colman *et al.*, 2020). Climate, especially temperature, tends to limit the range of areas suitable for laying eggs (Pike, 2013). Regionally, conditions that facilitate the migration of newborn hatchlings to estuary habitats, such as coastal areas close to marine currents, can influence nest density (Putman *et al.*, 2010; Okuyama *et al.*, 2011; Shillinger *et al.*, 2012; Putman, 2018). In terms of location, the topography of the beach plays important roles in the selection of the nesting area for sea turtles (Price *et al.*, 2018). This means that changes in lighting, sand dunes, vegetation, substrate and even the slope of the beach can harm the behavior of females (Maurer & Johnson, 2017) and consequently affect the reproductive success of the species (Fernandes *et al.*, 2016).

The return of females to land is directly linked to reproduction, as sea turtles bury their eggs under sandy beaches (Pike, 2013). Hatching eggs are extremely sensitive to water and thermal conditions within the nest and tolerate only small fluctuations in these variables (Ackerman, 1997; Davenport, 1997). After laying eggs, the development of embryos is subject to the influence of environmental factors highly dependent on the climatic conditions experienced during the incubation period (Monsinjon *et al.*, 2019). This means that hatching success and the sex determination of sea turtle hatchlings are intrinsically dependent on hatching temperatures.

According to experiments performed by Howard *et al.* (2014), hatching occurs within the thermal range of approximately 25-35 °C. Lower temperature limits lead to failure of embryos to develop and higher temperatures cause death. Still in the study by Howard *et al.* (2014), it was observed that nest temperatures can exceed 35 °C in some populations, occurring shortly before the emergence of the hatchlings. Even above the temperature, the eggs hatch successfully. Despite exceeding the tolerance range, hatchlings incubated in higher temperature nests may have lower hatching success, lower emergence rate and body size, higher rates of morphological abnormalities and/or reduced locomotor performance (Fisher *et al.*, 2014; Cavallo *et al.*, 2015). In addition, sea turtles have sex determination dependent on the cumulative effect of temperature, producing females at high incubation temperatures and males at low incubation temperatures (Yntema & Mrosovsky, 1980; Limpus *et al.*, 1985; Rafferty *et al.*, 2017; Montero *et al.*, 2018). Many nesting areas already produce

litters that are predominantly female, with some regions showing rates close to 100% (Hays *et al.*, 2017; Jensen *et al.*, 2018).

The increase in incubation temperatures causes a delay in male production, which may affect the long-term reproductive success of these populations (Fuentes *et al.*, 2011; Santidrián Tomillo *et al.*, 2012; Weber *et al.*, 2012; Monsinjon *et al.*, 2012; Monsinjon *et al.*, 2019). Current temperature levels likely reach or exceed the upper limit for successful hatchling development, as studies report poor hatching success on several nesting beaches (Rafferty *et al.*, 2010; Valverde *et al.*, 2010; Horne *et al.*, 2014; Rafferty *et al.*, 2014; Horne *et al.*, 2014; Rafferty *et al.*, 2017). As a result, warming temperatures are expected to put the reproduction of many sea turtle populations at risk.

Early tagging studies of sea turtles showed that females return to the same beaches they were born to nest (Carr & Ogren, 1960; Carr *et al.*, 1978). Philopatry is present in many taxa (Hueter *et al.*, 2005; Engelhaupt *et al.*, 2009; Rueger *et al.*, 2020; Ellis *et al.*, 2021), including sea turtles. Genetic studies reported that such nesting site fidelity was actually a philopatry, as the beaches used by females corresponded to the areas in which they were born (Meylan *et al.*, 1990; Allard *et al.*, 1994; Bowen & Karl, 2007). Philopatry in sea turtles, however, is not restricted to females, since it is also observed in males (Dutton *et al.*, 2013; Naro-Maciel *et al.*, 2014; Clusa *et al.*, 2018).

According to research, newborn hatchlings would be able to memorize different chemical and magnetic signals from the beaches from which they hatched and, during adulthood, use this information to find their home beach and reproduce (Lohmann *et al.*, 1997; Lohmann *et al.*, 2008; Lohmann *et al.*, 2013; Lohmann *et al.*, 2019). Furthermore, climate change can impact sea turtle populations due to their temperature sex determination (TSD) (Yntema & Mrosovsky, 1980). Global warming, when combined with philopatry, leads to an increase in the feminization of populations and the prevention of dispersal to cooler beaches as a countermeasure (Hawkes *et al.*, 2007; Witt *et al.*, 2010). The difficulty in colonizing new habitats may also be related to the probable niche imbalance caused by the Pleistocene glacial cycles, where the range and distribution of species were severely altered. (Hewitt, 2000; Dalén *et al.*, 2007; Foote *et al.*, 2013). Populations of the most varied taxa underwent recurrent phases of contraction and isolation during glacial events, undergoing

population expansion and secondary contact with previously isolated populations during interglacial periods (Hewitt, 2000).

Of the seven existing species of sea turtles, five of them are found on the Brazilian coast for feeding and reproduction, being them loggerhead turtle (*Caretta caretta*), green turtle (*Chelonia mydas*), leatherback turtle (*Dermochelys coriacea*), hawksbill turtle (*Eretmochelys imbricata*), and olive turtle (*Lepidochelys olivacea*) (Marcovaldi & Marcovaldi, 1999; ICMBIO, 2011). The species of sea turtle with the highest number of studies is the loggerhead turtle (*C. caretta*). It is widely distributed in tropical and temperate waters around the world (Pritchard & Trebbau, 1984) and is listed as vulnerable by the IUCN (Casale & Tucker, 2017). The loggerhead turtle (*C. caretta*) has a wide distribution and its geographic area for nesting regions is larger than that of other species of sea turtles, inhabiting the Atlantic, Indian, and Pacific Oceans, and the Mediterranean Sea (Spotila, 2004). The loggerhead turtle (*C. caretta*) is the most abundant species of sea turtle along the Brazilian coast (Marcovaldi & Marcovaldi, 1999). The species population located in Brazil is one of the largest in the world, behind Marisah, Oman, and eastern Florida, United States of America (Marcovaldi & Chaloupka, 2007). Its main nesting areas along the Brazilian coast are located in Sergipe, northern Bahia, northern Espírito Santo and northern Rio de Janeiro (Marcovaldi & Chaloupka, 2007). Regarding the genetic structure of loggerhead turtles (*C. caretta*) in Brazil, studies carried out by Reis et al. (2010) suggest the existence of two genetic stocks: the northern stock (Sergipe and Bahia hookeries) and the southern stock (Espírito Santo and Rio de Janeiro hookeries).

Although sea turtles are globally recognized as an endangered taxon, there are few efforts to assess the bioclimatic suitability of nesting grounds for loggerhead turtles (*C. caretta*). In the present article, we assessed how the niche of the loggerhead turtle (*C. caretta*) behaves globally, and focused on regular and sporadic nesting areas of loggerhead turtle (*C. caretta*) along the coast of Brazil, particularly to understand the probability of regular nestings in the Southern Subtropical Shelf (SSS) region. New sea turtles nesting records in southern Brazil are presented and bioclimatic suitability of the new locations in the extreme south of Brazil for nesting of loggerhead turtles in Brazil is evaluated. We aimed to provide further information on how loggerhead turtle populations may be impacted by climate change, exploring the influences of climatic variables on nesting grounds for the species in

the Atlantic Ocean, Pacific Ocean, Indian Ocean and Mediterranean Sea. This also allows us to assess whether the current distribution of loggerhead turtle (*C. caretta*) nesting areas are in bioclimatic imbalance or not.

2. Materials and methods

2.1. Study area

For the present work, nesting beaches along the coast of the oceans and the Mediterranean Sea were considered as the study area, focusing on the Southern Subtropical Shelf (SSS), from Cabo de Santa Marta Grande towards the border with Uruguay (~28°−34° S), because of the sporadic nesting occurrence in the region. The SSS coastline is 750 km long and consists of a near-continuous high-energy dissipative beach and backing barrier dominated by south-trending transgressive dunes, which in turn are backed by large freshwater lakes and lagoons (Short & Klein 2016).

2.2. Regular nesting beaches data

The dataset presented in this work includes the location of beaches used as nesting grounds for the loggerhead turtle and was obtained through OBI-SEAMAP (https://obisea-map seaturtle org), an online database that consists of an information system on oceanic biodiversity for ecological and spatial analysis of megavertebrate populations. The information was revised so that all nesting beaches of the species were included in the present study.

2.3. Search for evidence of sporadic subtropical nesting data

To investigate for evidence of sea turtle nestings in southern Brazil, we searched the literature and records obtained along 29 years of beach surveys on the northern Rio Grande do Sul (Southern Brazil) by the main local institutions. These surveys were mainly conducted to search for dead stranded marine tetrapods along the South Brazilian coastline. We

compiled databases from two complementary datasets and also searched for sporadic nesting records in the literature. In addition to the regular expeditions, specimens were also occasionally collected after the reporting of observed marine tetrapods by the local community.

Database 1 - Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul (GEMARS): A database from monthly beach surveys conducted to document occurrence patterns of stranded marine tetrapods between Torres (29° 20' S, 49° 43' W) and the Lagoa do Peixe National Park (31° 21' S, 51° 02'W, from January 1993 to December 2014. The sampling was well represented in all months and years of the study, and a total of 285 expeditions were carried out, covering 27194 km of surveyed beaches. Voucher specimens were deposited in the scientific collection of the GEMARS, the Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, and the Collection of Reptiles from the Department of Zoology, Universidade Federal do Rio grande do Sul (see Machado *et al.*, 2020).

Database 2 - Museu de Ciências Naturais (MUCIN/UFRGS): A database from weekly beach surveys, conducted between 2012 and 2019, to document occurrence patterns of stranded marine tetrapod in the State of Rio Grande do Sul (dataset 1). In alternating weeks, two complementary areas were searched: (a) 80 km from Itapeva in Torres (29° 21' S, 49° 44' W) to Imbé (29° 58' S, 50° 7' W), and (b) 50 km from Tramandaí (29° 58' S, 50° 7' W) to Dunas Altas in Palmares do Sul (30° 24' S, 50° 17' W). Beach surveys covered ~130 km of the SSS coastline every 15 d. The beach surveys were carried out using a 4-wheel drive pickup truck at a speed up to 40 km h−1, with 2−4 observers scanning the entire beach from the wash zone up to the base of the dunes. Live animals were transported to the wildlife rehabilitation center (CERAM) of the Centro de Estudos Costeiros, Limnológicos e Marinhos (CECLIMAR) from the Universidade Federal do Rio Grande do Sul (UFRGS) for veterinary care. Vouchers were housed in the scientific collections of the Museu de Ciências Naturais (MUCIN) from the UFRGS (see Tavares, Alvares & Borges-Martins, 2021 for additional information).

2.4. Bioclimatic variables selection

All data processing, analysis and mapping were performed in R software (R Core Team, 2021) with a combination of functions presented in Raster (Hijmans, 2022) and Humboldt (Brown, 2022) and following the methodology proposed by Vega *et al.* (2017) and Brown & Carnaval (2019). The study chose to use MERRAclim because the database covers oceanic and land areas on the same basis, which allowed us to delimit the coastline and buffer it into and out of the continents. We used 19 bioclimatic variables for three decades (1980, 1990 and 2000) based on remote sensing that are available in the MERRAclim dataset in spatial resolutions of 2.5 to 10 min (Vega *et al.*, 2017), namely: Annual Mean Temperature (BIO1), Mean Diurnal Range Temperature (BIO2), Isothermality (BIO3), Temperature Seasonality (BIO4), Max Temperature of Warmest Month (BIO5), Min Temperature of Coldest Month (BIO6), Temperature Annual Range (BIO7), Mean temperature of most humid quarter (BIO8), Mean temperature of least humid quarter (BIO9), Mean Temperature of Warmest Quarter (BIO10), Mean Temperature of Coldest Quarter (BIO11), Annual Mean Specific Humidity (BIO12), Specific Humidity of most humid Month (BIO13), Specific Humidity of least humid Month (BIO14), Specific Humidity seasonality (BIO15), Specific Humidity Mean of most humid quarter (BIO16), Specific Humidity Mean of least humid quarter (BIO17), Specific Humidity Mean of warmest quarter (BIO18) and Specific Humidity Mean of coldest quarter (BIO19). We used a 50 km buffer into and out of the coastal area around the continents to determine the region delimited by the occurrence set, with a latitudinal (48ºN-30ºS) cut (Fig. 2).

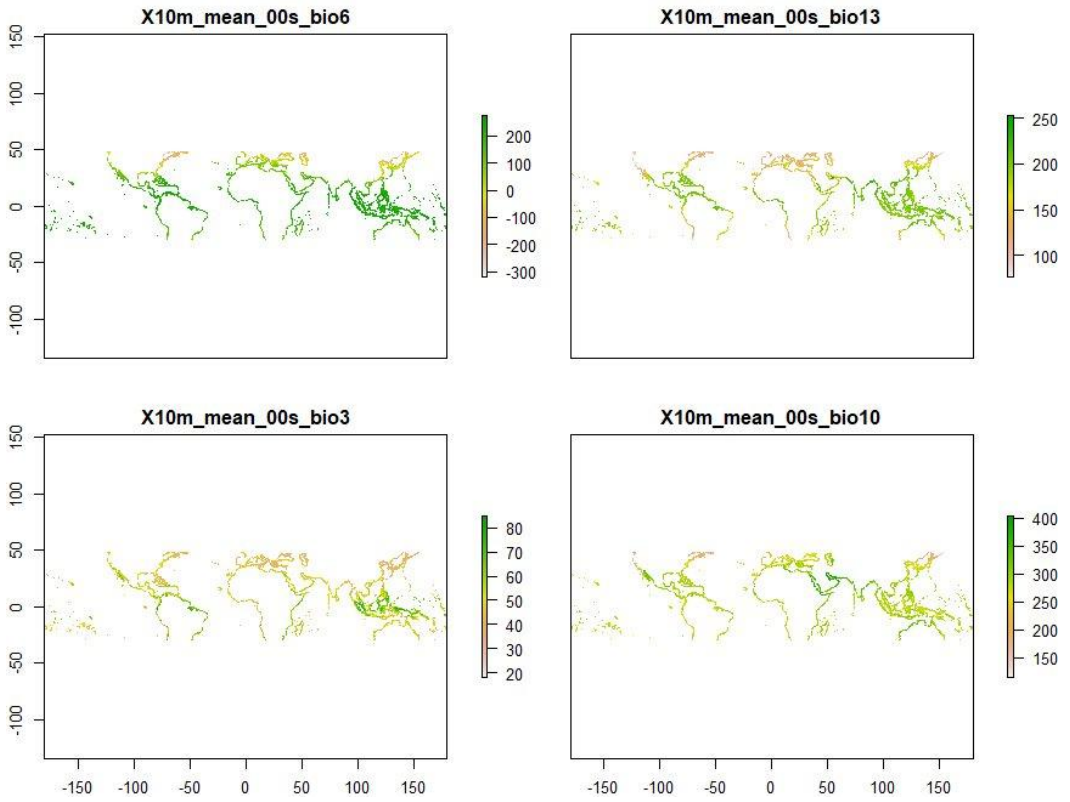


Fig. 2. Examples of four Bioclimatic layers from MERRAClim used for niche and distributional analyses. Data were restricted to coastal areas (50km inland + 50km inshore) and latitudinal interval of known nesting regions.

2.5. Statistical approach

For niche comparison, we followed the methodology proposed by Brown & Carnaval (2019) in the Humboldt (Brown, 2022) R Package (R Core Team, 2021). Details of input data and analysis parameters are given in the next sections. Niche equivalence and divergence tests were implemented to select the best set of occurrence data for Species Distribution Modeling and bioclimatic suitability inference.

The Niche Overlap Test (NOT) estimates the total environmental-space represented within the geographic distribution of the populations. It corresponds to an Equivalence statistic performed in the total accessible environmental-space of both species' geographic distributions and allows us to ask how equivalent the two populations' occupied niches are (Brown & Carnaval, 2019).

Niche Divergence Test (NDT) estimates the portion of the accessible environmental-space that is shared by both populations. NDT is, thus, the Equivalence and Background statistics performed in only analogous accessible environmental-space; it allows us to ask if the populations' niches are equivalent given a common environmental background (Brown & Carnaval, 2019).

2.6. Data preparation

Following the methodology proposed by Brown & Carnaval (2019) in the Humboldt R Package (Brown 2022), 19 environmental variables from MERRAClim (Vega *et al.*, 2017) were used for all sites of the Atlantic-Mediterranean population (envi1) and Indic-Pacific population (envi2) as the environmental data related to study areas 1 and 2. The nesting sites for loggerhead turtles were used for the Atlantic-Mediterranean population (sp1) in study area 1 (env1) and for the Indian-Pacific population (sp2) in study area 2 (env2). The resolution of the input environmental data (env.reso) in decimal degrees was obtained from the GIS data used to create the environmental data files (env1 and env2). Occurrences records closer than a minimum distance of 50 km to each other were removed (rarefy.dist=50; rarefy.units=km) to avoid spatial autocorrelation. To reduce the number of environment predictors and overcome multicollinearity issues, we ordered the 19 bioclimatic variables using a factor analysis with varimax rotation (Terrible *et al.*, 2012) selecting those most related to the four-first factors. Following Brown & Carnaval (2019) approach, environmental data needs to be previously selected in order to minimize overfitting problems. This selection was made using the humbold.top.env function based on method=”contrib” with ‘contrib.greater=5 parameters.

2.7. Accessible environments

Following Brown & Carnaval (2019), to perform the niche divergence test, the environmental inputs have to be trimmed to include only habitats accessible to the populations. We selected a 200km buffer around the nesting locations of populations 1 and 2 (env.trim.type = "radius")(trim.buffer.sp1 = 200 and trim.buffer.sp2 = 200 parameters).

2.8. Analogous and Non-analogous E-space

To trim environment inputs for the selection of analogous space, the parameter reduce.env=1 was used, where the second input environment (env2) was trimmed to match the first input (env1). Soon after, the trim type was based on two principal components (reducedtype="PCA"). The E-space that was not identical between the two habitats was trimmed considering the reduction for shared maximum and minimum habitats (reduce.env). Two niche equivalence analyzes were performed, one considering the analogous space (non.analogous.environments= "NO") and the other only the non-analogous space (non.analogous.environments="YES").

After accessible environments and analogous E-space are determined, the total space was used as the E-space of environments for both populations. The dimension with the most explained variance is called PC1 and plotted on the horizontal axes, the second-most explanatory dimension is called PC2 and placed on the vertical axis.

2.9. Quantifying niches

Point data were converted into a continuous surface to quantify population niches. For this, the surface shape (kern.smooth), the spatial resolution of the E-space (R) and the threshold at low suitability habitats (thresh.escape.z) were considered as part of the niches. Lastly, both species niches were plotted in a single plot (p.overlap=T), as well as the raw analysis data in a series of plots (p.scatter=T), and the E-space of both populations (p.boxplot=T).

2.10. Species Distribution Modeling (SDM)

A Maximun Entropy algorithm, Maxent 3.4.1 software (Phillips *et al.*, 2006; Phillips and Dudík, 2008), was used to model the potential bioclimatic suitability distribution of nesting beaches of loggerhead turtles around the world. We set Maxent to randomly select 75% of the occurrence localities as training data and the remaining 25% as testing of the

resulting models. Maxent algorithm predicts a distribution which tends to include the largest possible range size consistent with the occurrence data. The Receiver Operating Characteristic (ROC) and the Area Under the Curve (AUC) were used as measures of model performance. Bioclimatic variables (see Bioclimatic variables selection) and were selected to avoid model overfitting due to layers collinearity using a Varimax Rotated Analysis (VRA).

3. Results

3.1. Sporadic nestings on subtropical beaches in southern Brazil

1st record (*Caretta caretta*): We found one new record in a sporadic locality for loggerhead turtle in southern Brazil. On November 22, 2003, a female loggerhead turtle was found nesting (Fig. 3) on Praia de Rondinha (29° 30′ 39.492″ S, 49° 51′ 19.296″ W) in Arroio do Sal (RS, Brazil). The eggs were counted, totaling 143. On February 21st of 2004, the opening of the nest took place, where 53 were hatchlings (Fig. 4), 3 were stillborn, 38 embryos and 44 died.



Fig. 3. Female loggerhead turtle (*Caretta caretta*) nesting in Praia de Rondinha, Arroio do Sal (RS, Brazil). Record made on November 22, 2003.



Fig. 4. Hatchling loggerhead turtle (*Caretta caretta*) from Praia de Rondinha, Arroio do Sal (RS, Brazil). Record made on February 21, 2004.

2nd record (*Caretta caretta*): There is also evidence of a false crawl for the species on Praia Noiva do Mar (29° 50′ 23.712″ S, 50° 3′ 17.1″ W) in Xangri-lá (RS, Brazil). A turtle was seen returning to the sea around 11:00 am on November 11, 2020, where a trail was observed that extended to the dunes. The region was marked and verified, but no eggs were found.

We also found additional records of sporadic nesting of olive turtle (*Lepidochelys olivacea*) and leatherback turtle (*Dermochelys coriacea*) in southern Brazil.

3rd record (*Lepidochelys olivacea*): For the olive turtle, on February 03, 2018, a female was found nesting on Praia de Arroio Teixeira (29° 38′ 44.148″ S, 49° 56′ 51.764″ W) in Capão da Canoa (RS, Brazil). The eggs were counted, totaling 116. On May 10th, the nest was opened, where 20 were hatchlings, 33 were stillborn, and 52 were embryos.

4th record: On December 18, 2009, a female leatherback turtle was found alive on the edge of Praia Curumim (29° 38′ 5.37″ S, 49° 56′ 27.876″ W) in Capão da Canoa (RS, Brazil). She was in perfect condition, which allowed her to be considered on the beach as a possible

nesting attempt. She was taken to CECLIMAR and stayed at CERAM for three days, being released only on December 21th with the help of a MUNDIAL Serviços Marítimos LTDA vessel.

5th record: Another record for leatherback turtle was documented on January 12, 2021 at 1:00 am at Guarita 40 do Farol (29° 33′ 54.504″ S, 52′ 56.892″ W) in Arroio do Sal (RS, Brazil). Crawl marks were spotted and the nest was then explored the next morning. Three eggs were collected for incubation and laboratory follow-up.

6th record: The same turtle (from 5th record) was documented nesting for the second time on January 24, 2021 at 01:30 am at Praia Valverde (29° 9′ 23.544″ S, 49° 34′ 29.604″ W) in Balneário Gaivota (SC, Brazil). The same leatherback turtle can spawn from three to seven spawns during the breeding season, with a spacing of up to 50 km between nests (Miller, 1997; Bell *et al.*, 2004; Stewart & Johson, 2006). From the nesting of Arroio do Sal, we had made a projection that a new nest would be possible between Balneário Gaivota (SC, Brazil) and Tramandaí (RS, Brazil). And indeed the turtle confirmed our expectation. The estimate was that there were 80 eggs at least. On January 26, 2021, a visit was made to the site, where the existence of the nest was confirmed.

7th record: In the period of the third nesting, between February 01 and 06, 2021, there were two days of strong undertow. Despite the undertow having occurred in the two nesting sites of the leatherback turtle, the nests were not affected, as they were built in the dunes by the turtle. On February 9, crawling traces were found 5 km north of the second nesting site. Thus, it is considered that the third nesting from the same turtle from 5th and 6th record took place at the turn of the 8th to the 9th of February at Praia Valverde (29° 12′ 5.76″ S, 49° 36′ 48.888″ W) in Balneário Gaivota (SC, Brazil).

Among the data searched in the literature, two leatherback turtle nests were found.

8th record: The female leatherback turtle was found at Praia do Paraíso (29° 26′ 0.996″ S, 49° 47′ 54.996″ W) in Torres (RS, Brazil) at 00:40 on January 01, 1995. The hatching occurred on March 5th, after 64 days of incubation. Hatchlings were observed, but the nest could not be accurately located (Soto *et al.*, 1997).

9th record: The leatherback turtle nesting took place on the Entremares Platform, Balneário Rincão (28° 51′ 32.004″ S, 49° 16′ 6.996″ W) in Içara (SC, Brazil). Local residents witnessed the event (emergence from the sea, preparation of the nest, egg-laying, return to

sea), which lasted about three hours. After 60 days of incubation, the nest was exhumed. None of the 104 eggs showed embryonic development (Soto *et al.*, 1997).

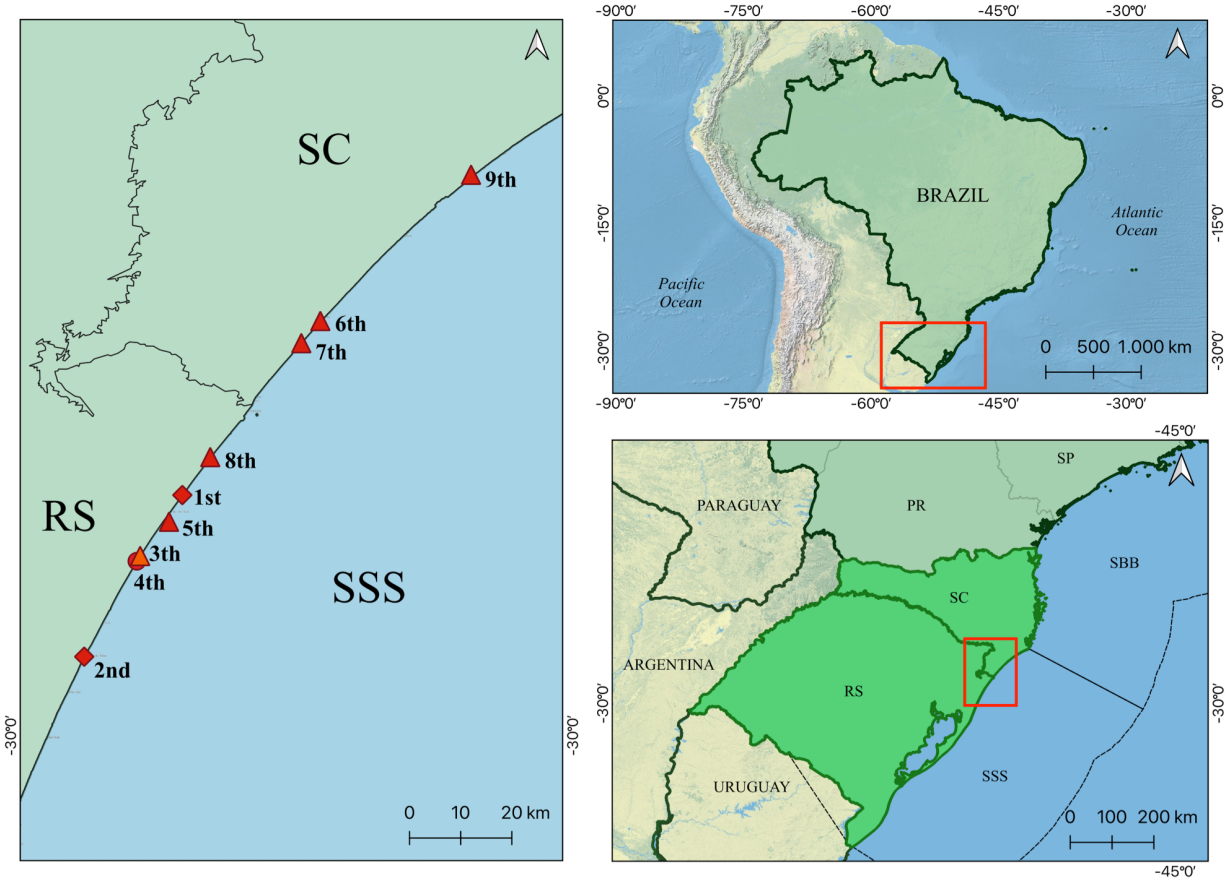


Fig. 5. (Left) Occurrence of sporadic sea turtle nesting in the Southern Subtropical Shelf (SSS), where triangles are for leatherback turtles (*Dermochelys coriacea*), diamond is for loggerhead turtle (*Caretta caretta*), and circle is for olive turtle (*Lepidochelys olivacea*). Red means nesting site and orange female in healthy condition, but without evidence of nesting. (Top right) Map of Brazil focusing on the Southern Subtropical Shelf (SSS), the study area of the present work. (Bottom right) Map of Southern Brazil, showing part of the Southern Subtropical Shelf (SSS) as an area of occurrence for sporadic nesting of sea turtles in Santa Catarina (SC) and Rio Grande do Sul (RS).

3.2. Niche Overlap Test (NOT)

A total of 13 bioclimatic layers was selected as predictors for the niche comparisons: BIO1, BIO5, BIO4, BIO6, BIO8, BIO9, BIO10, BIO12, BIO13, BIO15, BIO16, BIO18, and BIO19. Our PCA reveals that 86.12% (or separately, PC1= 64.56% and PC2= 21.52%) of the variance in our environmental data input can be represented in a 2-dimensional E-space. (Fig. 6).

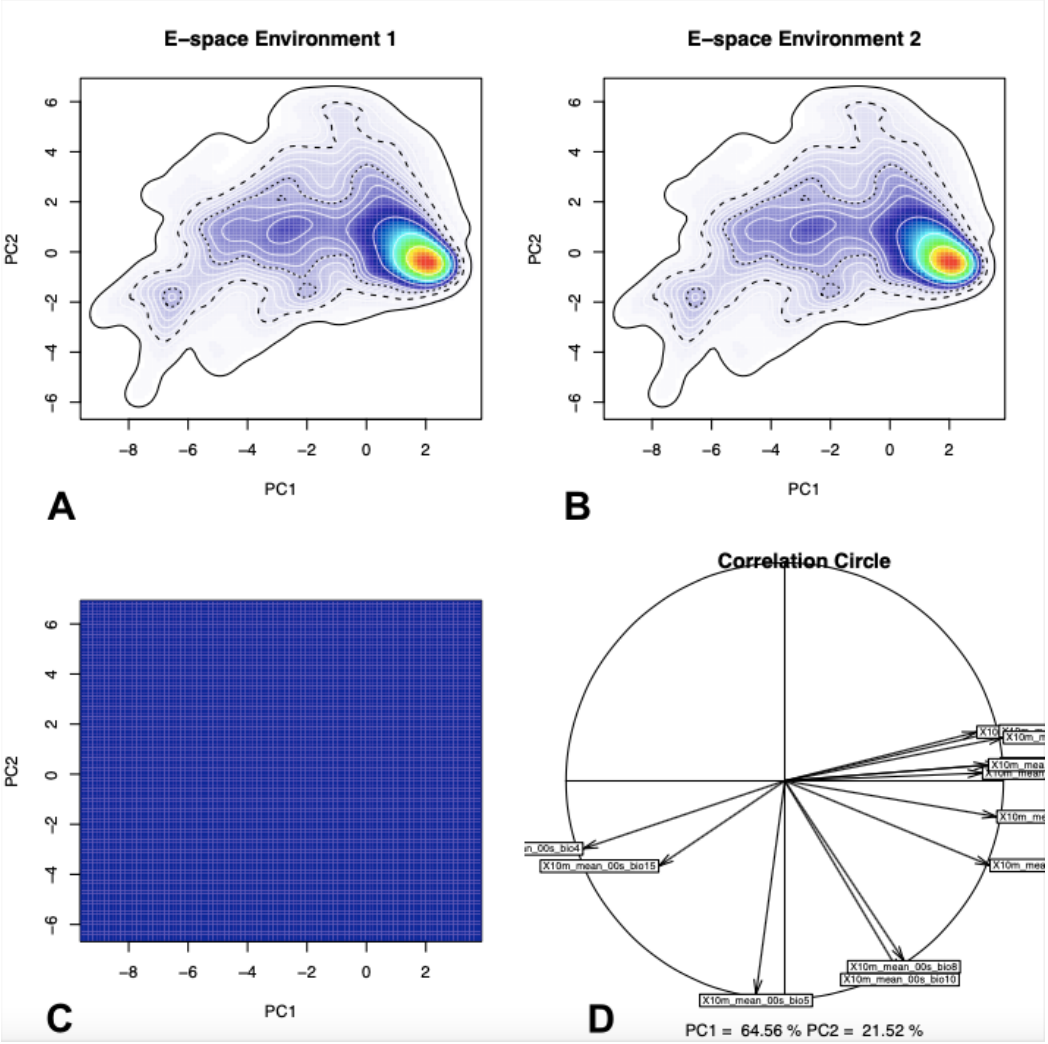


Fig. 6. (A & B) Total space as plots of E-space of Environment 1 (Atlantic-Mediterranean) and Environment 2 (Indian-Pacific). Raw environmental-space is converted to a kernel density representing the populations' occupied E-space. (C) Total Environment in E-space. Since there is no difference between Environment 1 and 2, the space is fully represented by the blue color. (D) E-space correlation circle of original data. PCA of the variance in

environmental space represented in a 2-dimensional E-space. 13 of the 19 bioclimatic variables are projected Inside the 2-dimensional circle.

Loggerhead turtle nesting beaches occupy only a fraction of the available E-space in tropical and subtropical coastal regions around the world. The nesting populations from the Atlantic-Mediterranean occupy a wider range of the global coastal E-space than the Indian-Pacific, as can be seen in Fig. 7A and 6B. Both populations show signs of bioclimatic disequilibrium, as suggested by the higher values skewed distribution of the realized vs. available space on PC1 (Fig. 7).

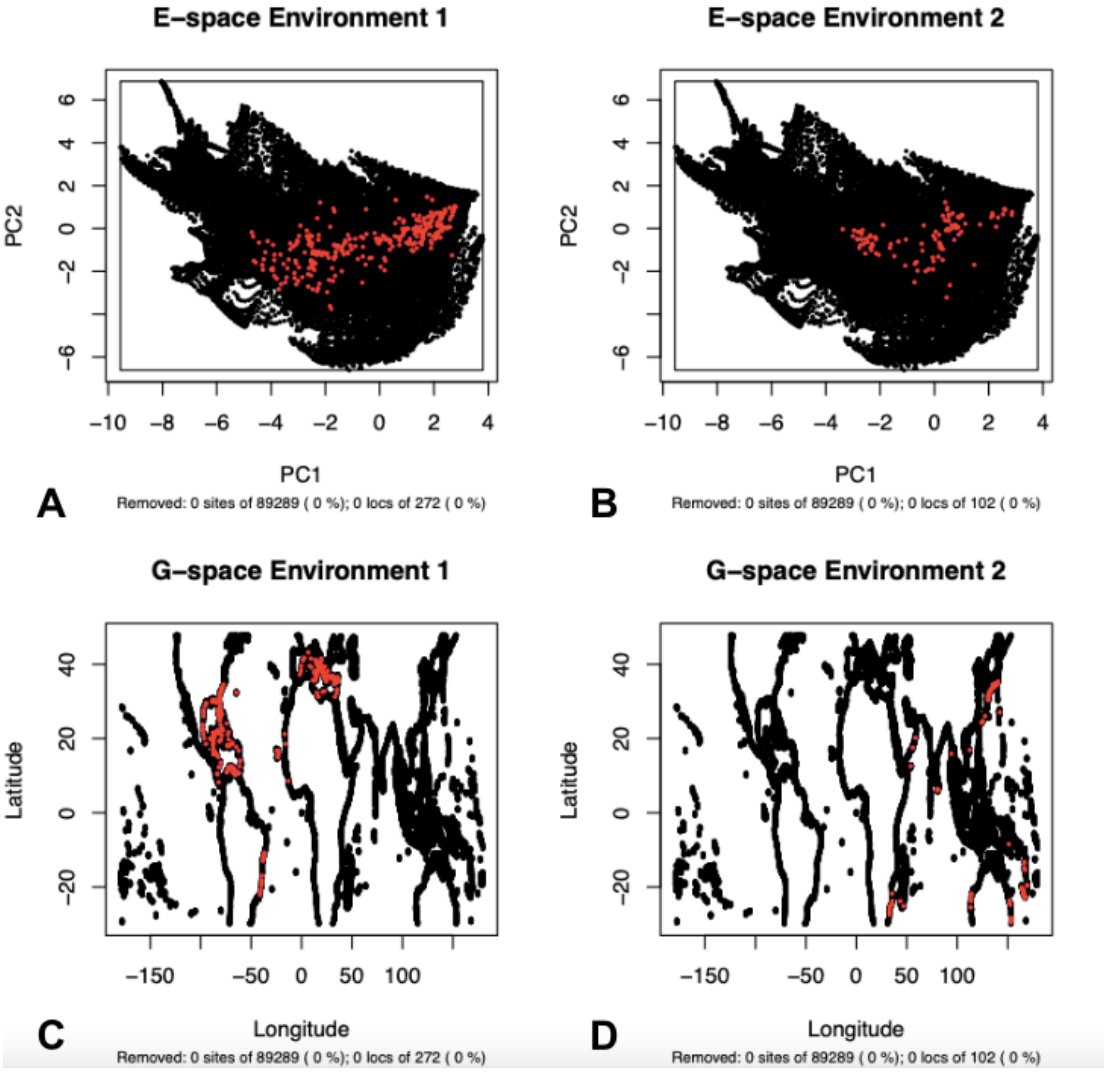


Fig. 7. (A & B) Plots of G-space vs. Total E-space of Environment 1 (Atlantic-Mediterranean) & 2 (Indian-Pacific). (C & D) The total analogous E-space is

plotted in G-space, where red points are occurrence localities in the total E-space and black points represent the total E-space environment.

With the Niche Equivalency Test, the observed niche similarity between populations 1 and 2 is then assessed against the null distribution. The significant value (p.value = 0.0099) indicates that the null hypothesis is rejected, so populations' niches are non-equivalent (Fig. 8). The nesting bioclimatic niches in the Atlantic-Mediterranean are different from the Indian-Pacific.

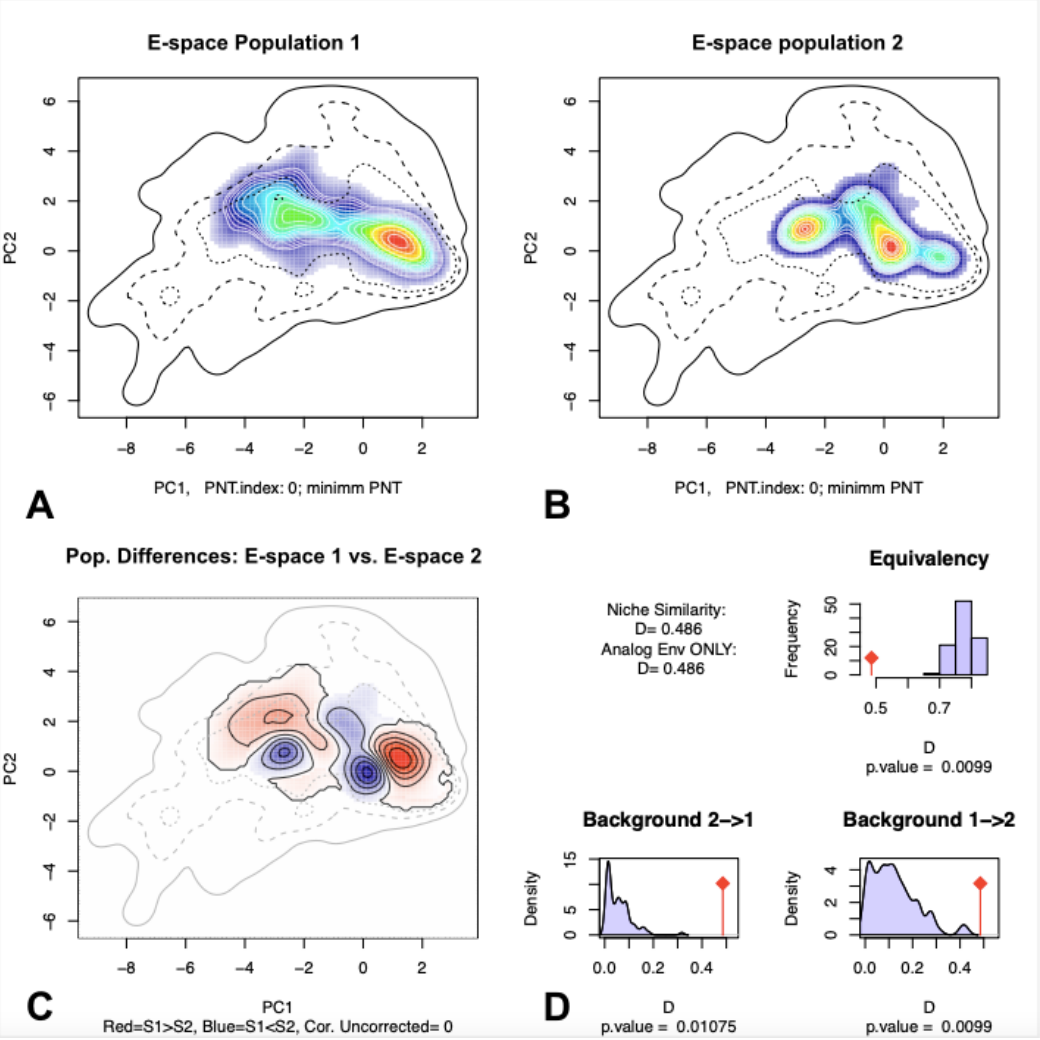


Fig. 8. (A) Plot of E-space for Population 1 (Atlantic-Mediterranean). Raw environmental-space is converted to a kernel density representing the populations' occupied E-space. (B) Plot of E-space for Population 2 (Indian-Pacific). Raw environmental-space is converted to a kernel density representing the populations' occupied E-space.. (C) The difference between environmental E-space and populations' E-space is quantified, and

correlations among these differences are assessed. The red and blue coloration in plots depict areas where that E-space is more abundant in environment 1 and environment 2, respectively. (D) Occurrence localities are pooled and resampled in two groups equaling the number of localities in each to assess the significant equivalence of both populations' distributions. Niche similarity is assessed and compared to the niche similarity of the observed data. Significance is determined by the frequency that the observed overlap is greater than the reshuffled datasets. The Background statistic asks if the two distributed populations are more different than expected given the underlying environmental differences between the regions in which they occur. The function compares the observed niche similarity between populations 1 and 2 to the overlap between population 1 and the random shifting of the spatial distribution of population 2 in geographic space. It then measures how that shift in geography changes the occupied environmental-space.

With the Background Test, the observed values of the background similarity obtained from the two original populations were significantly lower than expected from the randomly shifted null distribution (p.value = 0.01075 for Background 2 -> 1) and non-significant (p.value = 0.0099 for Background 1 -> 2), which means that the null hypothesis of background similarity between populations is supported (Fig. 8).

The Niche Overlap Test has rejected the null hypothesis of niche equivalency, showing evidence that the populations 1 (Atlantic-Mediterranean) and 2 (Indian-Pacific) are not equivalent when considering the total E-space for both of them (Fig. 9).

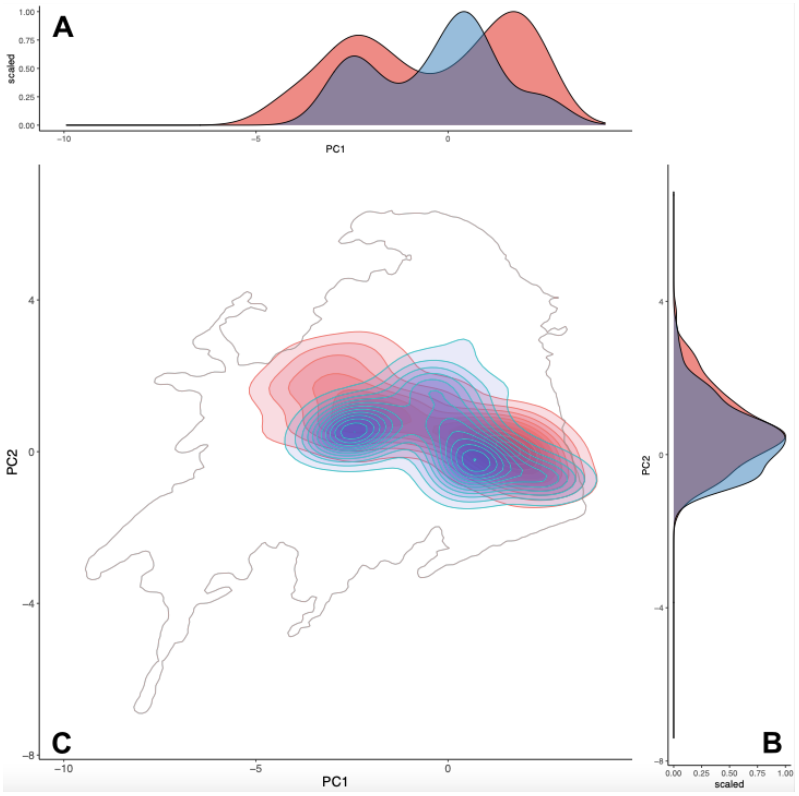


Fig. 9. (A & B) Plot of both populations (Atlantic-Mediterranean & Indian-Pacific) in E-space. For each PC, the density of each population is displayed. (C) Filled Kernel Density Isopleths (red = pop1 and blue = pop2).

3.2. Niche Divergence Test (NDT)

A total of 13 bioclimatic layers was selected as predictors for the niche comparisons: BIO1, BIO5, BIO4, BIO6, BIO8, BIO9, BIO10, BIO12, BIO13, BIO15, BIO16, BIO18, and BIO19. Our PCA reveals that 84.90% (or separately, PC1= 58.93% and PC2= 25.97%) of the variance in our environmental data input can be represented in a 2-dimensional E-space (Fig. 10).

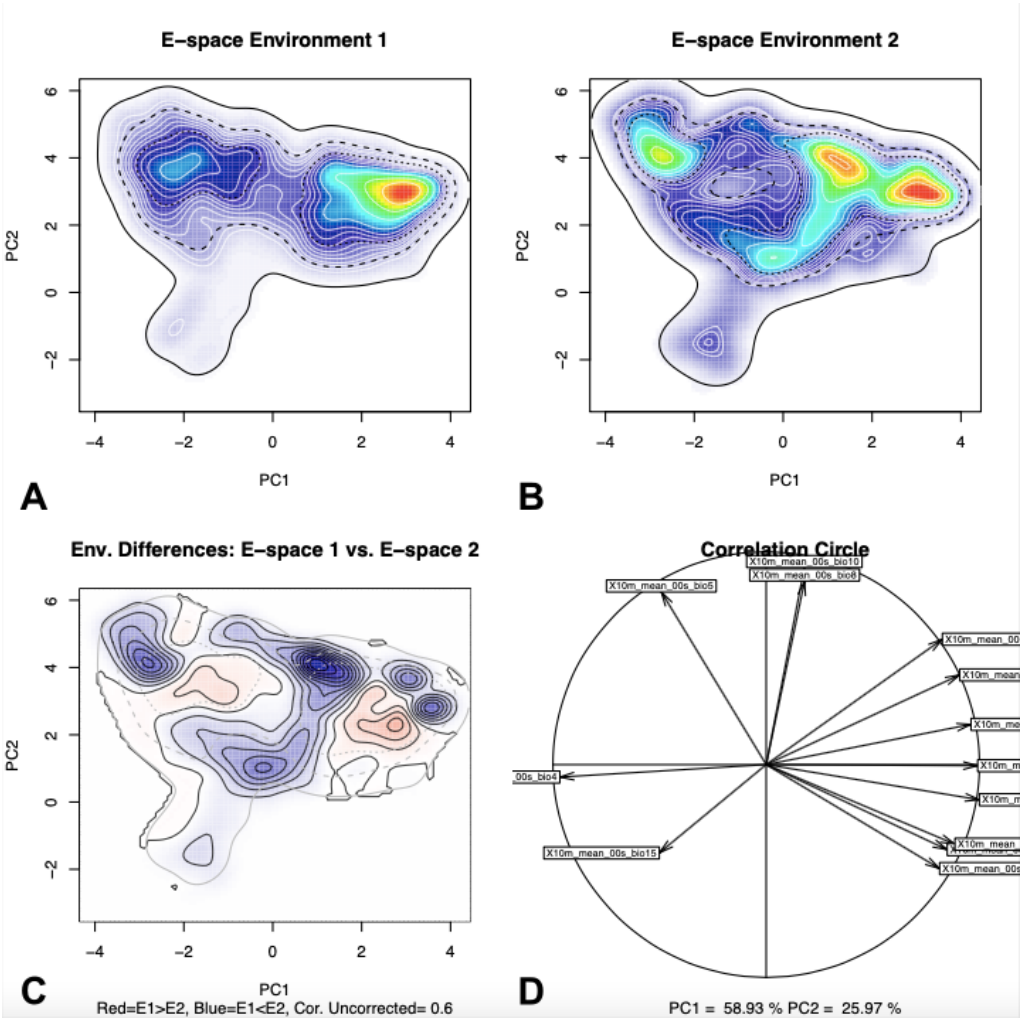


Fig. 10. (A) Plot of E-space for Environment 1 (Atlantic-Mediterranean). Raw environmental-space is converted to a kernel density representing the population's occupied E-space.. (B) Plot of E-space for Environment 2 (Indian-Pacific). Raw environmental-space is converted to a kernel density representing the populations' occupied E-space. (C) The difference between environmental E-space and species' E-space is quantified, and correlations among these differences are assessed. The red and blue coloration in plots depict areas where that E-space is more abundant in environment 1 and environment 2, respectively. (D) E-space correlation circle of original data. PCA of the variance in environmental space represented in a 2-dimensional E-space. Bioclimatic variables are projected Inside the 2-dimensional circle.

Loggerhead turtle nesting beaches occupy most of the available accessible E-space. The nesting populations from the Mediterranean occupy a rather different range of E-space,

as can be seen in Fig. 11A. Most records from the Mediterranean were removed from the niche comparison, as they represent non-analogous E-space (Fig. 11).

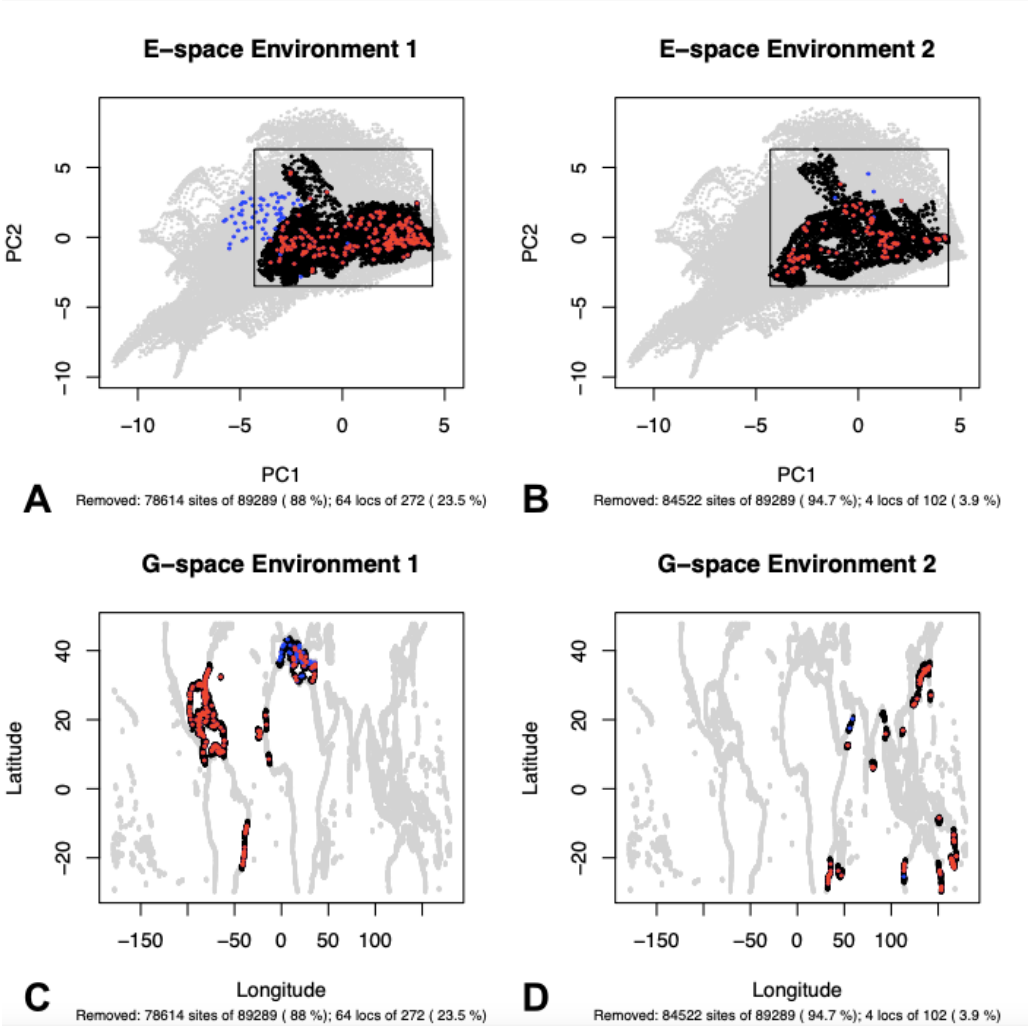


Fig. 11. (A) Plots of G-space vs. Total E-space of Environment 1 (Atlantic-Mediterranean). (B) Plots of G-space vs. Total E-space of Environment 2 (Indian-Pacific). (C) The analogous E-space for Environment 1 (Atlantic-Mediterranean) is plotted in G-space. (D) The analogous E-space for Environment 2 (Indian-Pacific) is plotted in G-space. The black box depicts shared E-space, red points are occurrence localities retained after E-space is reduced to analogous environments, blue points are occurrence localities removed after E-space is reduced to analogous environments, grey points aree E-space retained after E-space is reduced to analogous environments, and white points are E-space removed after E-space is reduced to analogous environments.

After accessible environments and analogous E-space were determined, we quantified the E-space of the populations. Abundances of E-space for population 1 (Atlantic-Mediterranean) and 2 (Indian-Pacific) were represented by two colors (Fig. 12), in which blue colors are where population 2 has higher abundances of corresponding E-space and red colors are where population 1 has higher abundances of corresponding E-space. The Niche Similarity was calculated by Schoener's D Niche Similarity test and is not significant (D= 0.398), indicating that the niches are equivalent (Fig. 12).

With the Niche Equivalency Test, the observed niche similarity between population 1 and 2 is then assessed against the null distribution. The non-significant value (p.value = 0.25743) states that the two population datasets are statistically equivalent and accepts the null hypothesis that populations' niches are equivalent (Fig. 12).

With the Background Test, The observed values of the niche similarity obtained from the two original populations were significantly lower than expected from the randomly shifted null distribution (p.value = 0.03448, and p.value = 0.00164), which means that the null hypothesis that similarity between populations is supported (Fig. 12).

The occupied niche equals the fundamental niches of both populations and both populations' accessible environments contained the other fundamental niche, so the Niche Overlap and Niche Divergence tests have rejected the null hypothesis of niche equivalency, showing evidence that the populations 1 (Atlantic-Mediterranean) and 2 (Indian-Pacific) are not equivalent when considering the available E-space for both of them (Fig. 12).

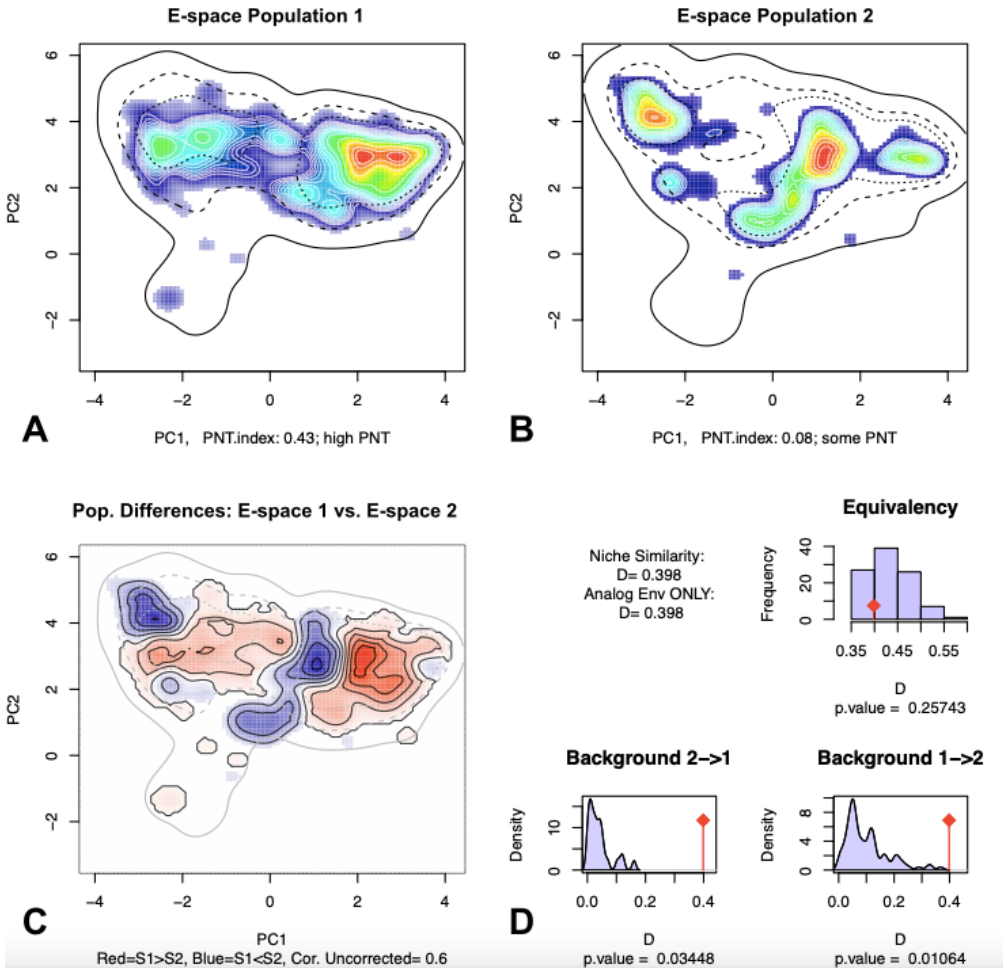


Fig. I2. (A) Plot of E-space for Population 1 (Atlantic-Mediterranean). Raw environmental-space is converted to a kernel density representing the population's occupied E-space. (B) Plot of E-space for Population 2 (Indian-Pacific). Raw environmental-space is converted to a kernel density representing the population's occupied E-space. (C) The difference between environmental E-space and species' E-space is quantified, and correlations among these differences are assessed. The red and blue coloration in plots depict areas where that E-space is more abundant in environment 1 and environment 2, respectively. (D) Niche Similarity, Equivalency, and Background values. (D) Occurrence localities are pooled and resampled in two groups equaling the number of localities in each to assess the significant equivalence of both populations' distributions. Niche similarity is assessed and compared to the niche similarity of the observed data. Significance is determined by the frequency that the observed overlap is greater than the reshuffled datasets. The Background statistic asks if the two distributed populations are more different than expected given the underlying environmental differences between the regions in which they occur. The function

compares the observed niche similarity between populations 1 and 2 to the overlap between population 1 and the random shifting of the spatial distribution of population 2 in geographic space. It then measures how that shift in geography changes the occupied environmental-space.

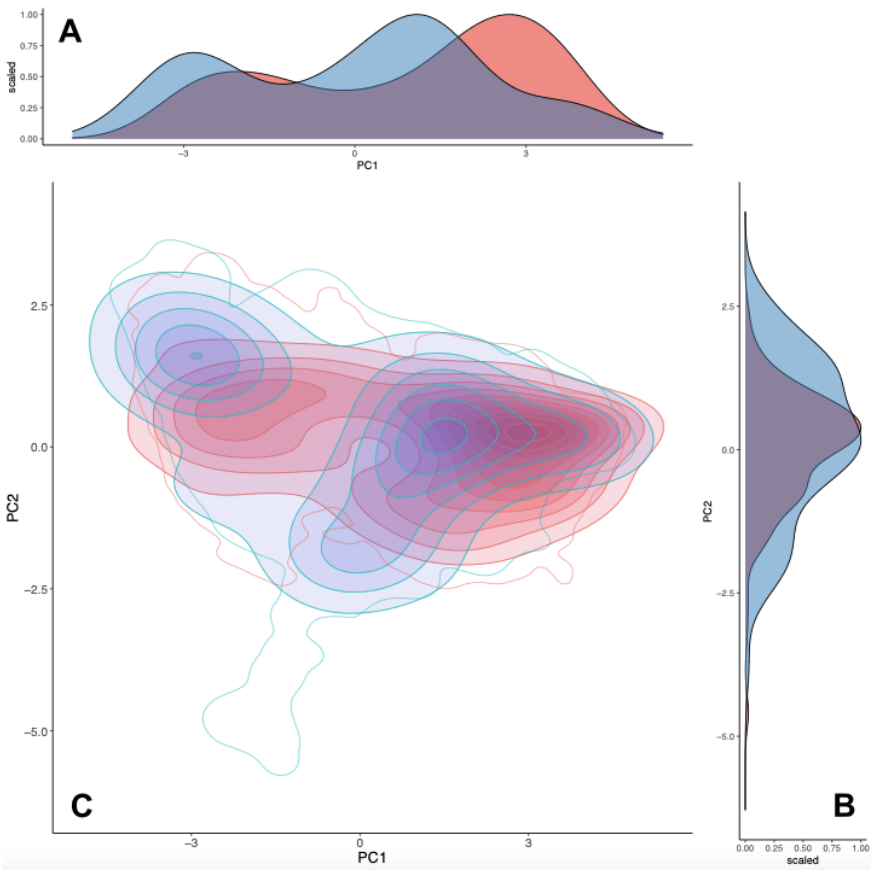


Fig. 13. (A & B) Plot of both populations (Atlantic-Mediterranean & Indian-Pacific) in E-space. For each PC, the density of each population is displayed. (C) Filled Kernel Density Isopleths (red = pop1 and blue = pop2).

3.3. Bioclimatic Suitability of nesting beaches around the world

Given the absence of evidence of niche divergence between loggerhead turtle populations in different oceans, we considered that a global Species Distribution Model is the best estimate of potential bioclimatic niche for the species. Four bioclimatic layers were selected for running the models, BIO03, BIO06, BIO10, and BIO13. Niche models generated

in MAXENT for the global distribution of loggerhead turtle (*C. caretta*) nesting beaches returned a large area of intermediate suitability values along the tropical and subtropical coasts around the world (Fig. 14). Area Under the Curve was equal to 0.824 and the most frequent suitability values was around 0.6 limit. Along the entire Brazilian coast, suitability was homogeneous and ranged between 0,65 and 0,55 (Fig. 15). In the global model, higher suitability values were mostly intermediate (~0.6) and many nesting beaches occur in low suitability regions, as low as ~0.4 (Fig. 16). The suitability estimated for the area with the only confirmed effective sporadic nesting in southern Brazil was lower than the average of regular nestings in Brazil. However, the suitability in southern Brazil is comparable to some regular beaches in Brazil, and is higher than many regular beaches in the North Atlantic/Mediterranean, Indian and Pacific Oceans.

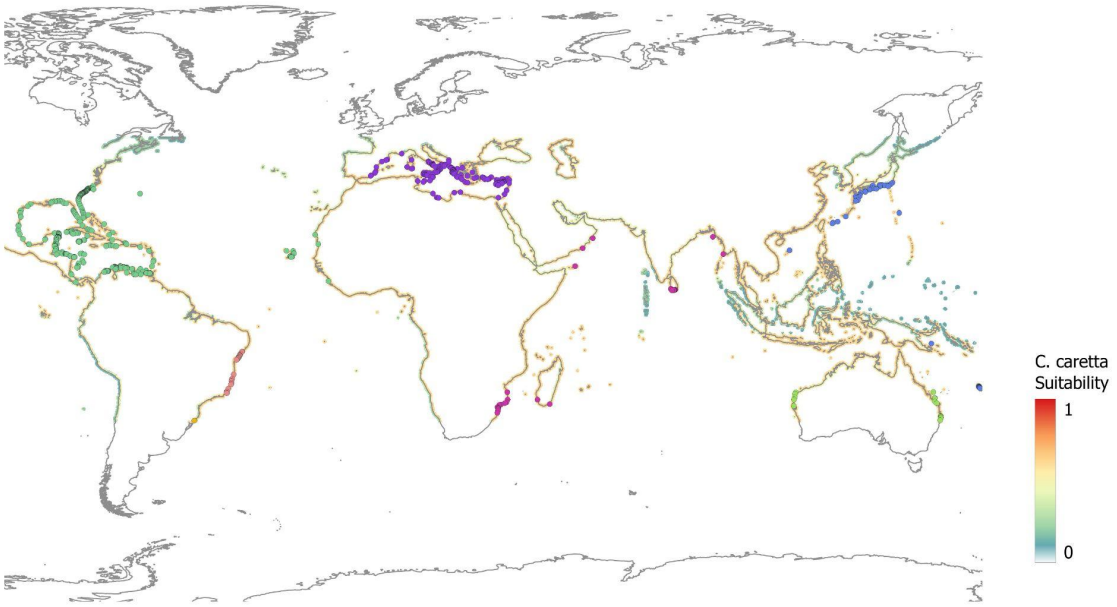


Fig. 14. Global bioclimatic suitability for loggerhead turtle (*C. caretta*) nestings around the world estimated with Maxent. Points represent regular nesting beaches. Cyan is for the North Atlantic population, Purple is for the Mediterranean Sea population, Pink is for the Indian Ocean population, Blue is for the Pacific Ocean population, and Green is for the Australian population.

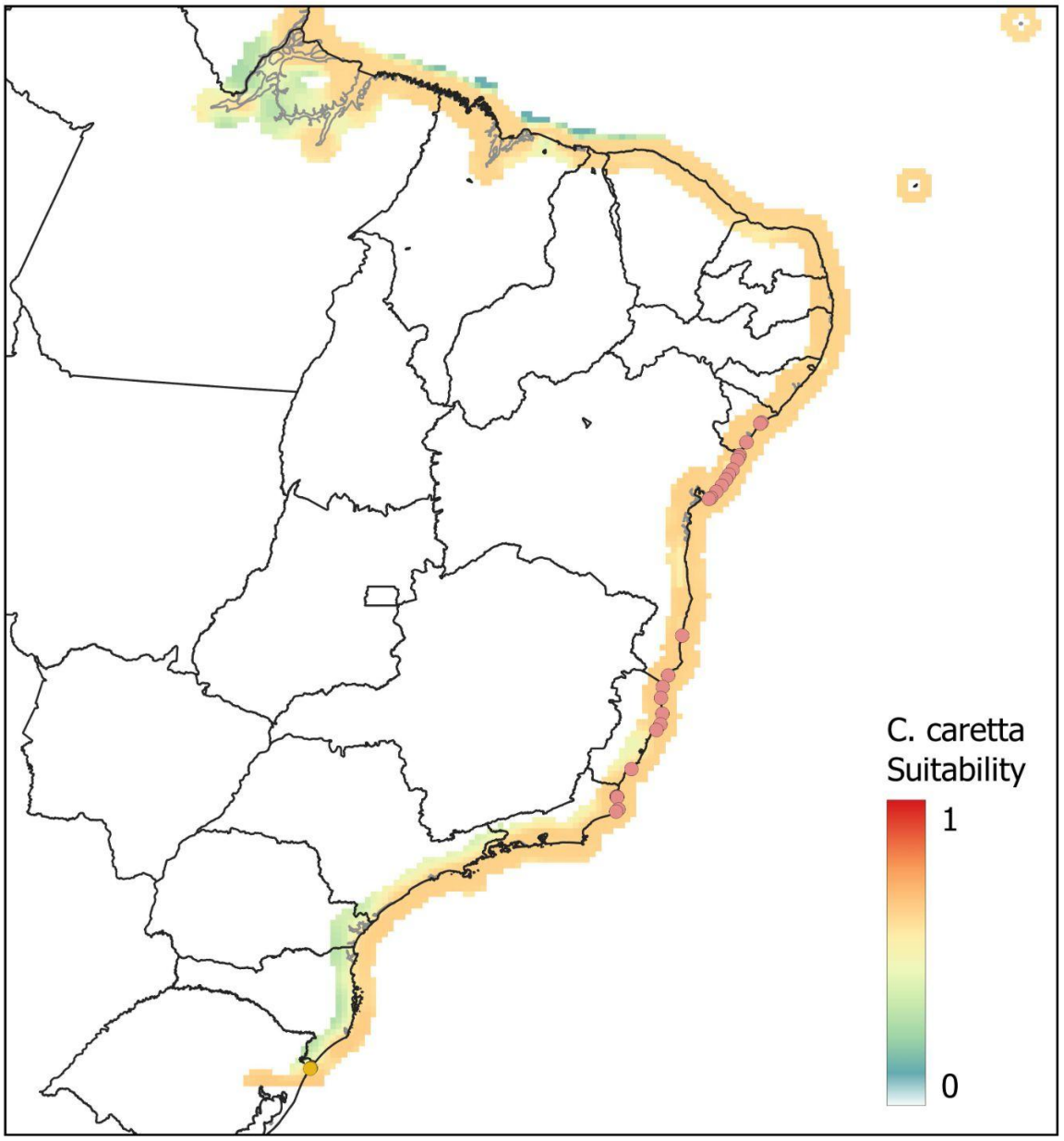


Fig. 15. Bioclimatic suitability for loggerhead turtle (*C. caretta*) nestings along the Brazilian coast, estimated with Maxent. Points represent regular nesting beaches (pink) and sporadic nesting in Praia da Rondinha, RS, southern Brazil (yellow).

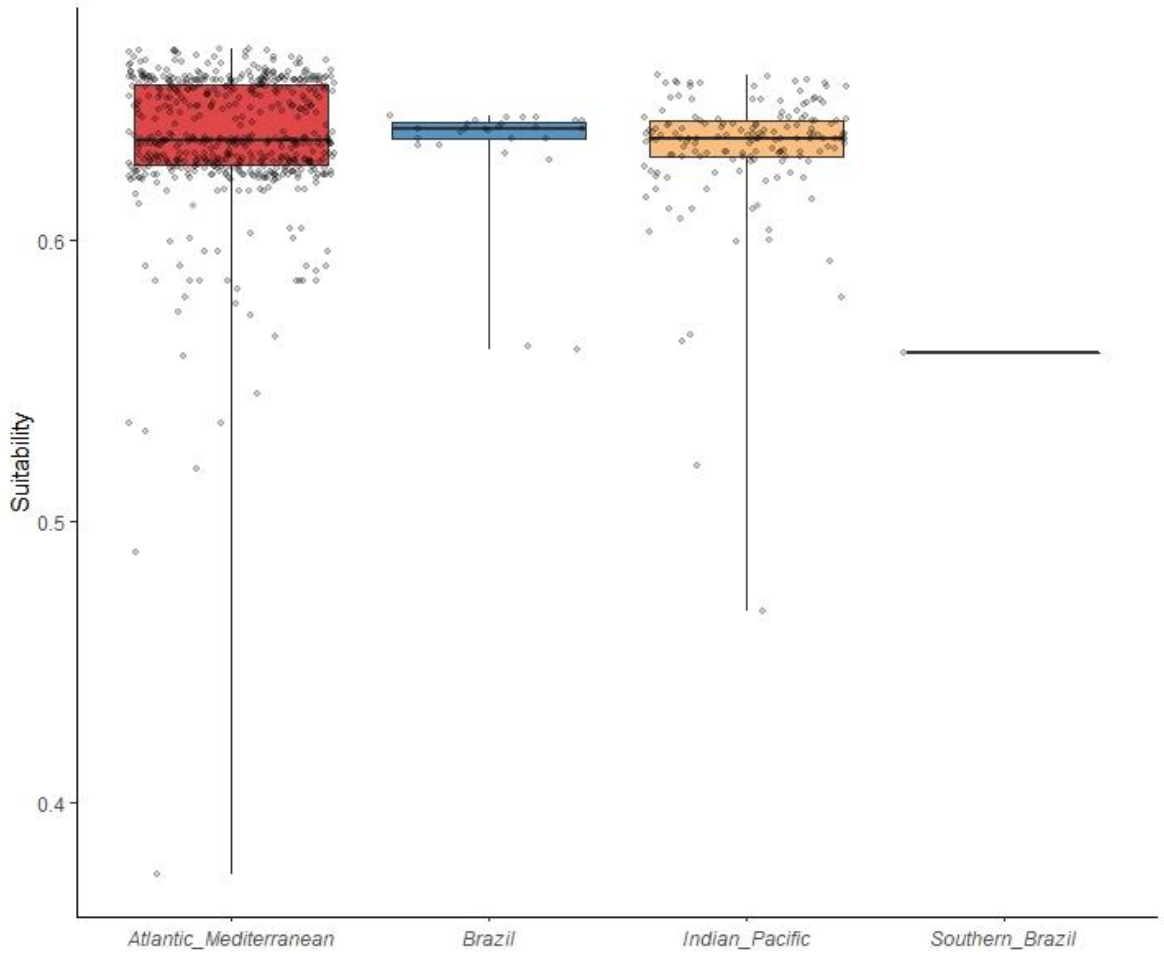


Fig. 16. Comparison of bioclimatic suitability of loggerhead turtle (*Caretta caretta*) nesting beaches between North Atlantic/Mediterranean sea, Indian/Pacific, Brazil (regular nestings) and occasional nesting (southern Brasil).

4. Discussion

The loggerhead turtle (*C. caretta*) is a widely distributed species, with nesting occurring in tropical, subtropical and temperate environments throughout all oceans (Pritchard & Trebbau, 1984; Marcovaldi & Chaloupka, 2007). To understand the suitability of the species, the Niche Overlap Test analyzes were first performed (Brown & Carnaval, 2019). We found that the Atlantic-Mediterranean (population 1) and Indian-Pacific (population 2) niches are not equivalent. Particularly the Mediterranean nesting beaches occupy a different environmental space (E-space). However, when performing the Niche Divergence Test, no evidence was found that they have diverged and differences can be the result of available E-space and biogeography. According to Brow & Carnaval (2019), this difference demonstrates that measurements in geographic space are only accurate when environmental variables are equally represented in the geographical space (G-space). In natural systems, environmental variables are similarly perturbed, leading researchers to overestimate or underestimate niche similarity based on the distribution of key environmental space across geography. Our results suggest that the loggerhead turtle (*C. caretta*) may even occupy different niches, but this reason may be more related to the biogeography and behavior of the species - mainly taking into account the changes in distribution throughout the Pleistocene (Hewitt, 2000; Dalén *et al.*, 2007; Foote *et al.*, 2013) and due to the high factor of philopatry in sea turtles (Meylan *et al.*, 1990; Allard *et al.*, 1994; Bowen & Karl, 2007), making them respond slowly to climate change (Deutsch *et al.*, 2008; Tewksbury *et al.*, 2008).

When looking at the occupation of the niche (Fig. 7) where the accessible environment by species was taken into account, most of the occupation of the Atlantic-Mediterranean niche is in the extreme right of the available environment area (high PC1 values). This indicates that the Atlantic-Mediterranean, especially the North and South Atlantic nesting beaches, are at bioclimatic moderate risk. This indicates that the Atlantic-Mediterranean niche may be more bioclimatically imbalanced compared to the Indian-Pacific (population 2), where there is a lower concentration in a specific area (Brown & Carnaval, 2019).

As it was identified that there is no evidence of niche divergence, the best model to estimate the bioclimatic suitability of nesting beach distribution is a global model, assuming all occupied E-space as part of the bioclimatic plasticity of loggerhead turtles. Perhaps because the loggerhead turtles occupy such diverse environments and because of the evidence that it may be in disequilibrium, the result showed a wide zone of suitability for nesting in the world, although all areas have intermediate suitability potencial (Fig. 13).

Sporadic nesting areas for loggerhead turtles (*C. caretta*) in the extreme south of Brazil are 1,217.81 km away from the nearest regular area, located on the north coast of Rio de Janeiro (Marcovaldi & Chaloupka, 2007). In fact, the hatching success of loggerhead turtles in southern Brazil was much lower when compared to the country's regular nesting grounds. In the present study, a hatching success rate of 37% was found for the first record of sporadic nesting. The average hatching success is 78.6% ± 19.7 in Rio de Janeiro, 78.5% ± 19.3 in Espírito Santo and 73.8% ± 19.3 in Bahia (Montero *et al.*, 2018).

As expected, the areas located in the Southern Subtropical Shelf (SSS) were shown to have lower suitability, being equivalent to the lowest suitability for nesting loggerhead turtles (*C. caretta*) in Brazil, but still superior to the suitability of many regular nesting areas around the world. (Fig. 15). The regions in the extreme south of Brazil may be important areas to continue looking for sporadic nesting and even to identify the presence of putative new micropopulations. Currently, there is no monitoring effort aimed at this objective, as the occurrences are very rare. However, the intense monitoring of beaches nowadays focused mainly on recording strandings (Tavares, Janish & Borges-Martins, 2021), combined with the intense effort of several scientific institutions, has allowed local communities to assist in these searches. Residents who know the institutions and their research led researchers to identify nesting areas in increasing numbers. A citizen science approach can bring new information about sporadic nestings and engage the local community in the conservation of an biologically relevant area (Vieitas *et al.*, 1999; Ferraro & Gjertsen, 2009; Awabdi *et al.*, 2018).

As higher numbers of sporadic nesting have been found over the last few years thanks to the current effort to monitor beaches and the increase in reports by local citizens, the areas present in the SSS could become more important as global warming transforms them into areas more suitable than even areas in the north of Brazil (Monsinjon *et al.*, 2019).

Unfortunately, the historical colonization speed of sea turtles is very slow and should not be able to respond to climate changes that occur on smaller and faster scales, such as in tens of years. In severe cases of loss of suitability, assisted migration (or colonization) of nesting sites by moving eggs to more suitable areas (Bowen *et al.*, 1994) can be proposed, with the SSS being an interesting region to assist in the conservation of sea turtles. The strategy, however, is based on sea turtles' natal homing behavior, which is still controversial and requires, among others, an extensive ecological understanding of the species and a careful characterization of new intended habitats (Dade *et al.*, 2014; McLachlan *et al.*, 2007).

According to Monsinjon *et al.* (2019), sea turtles are unlikely to rapidly change their nesting sites because of their natal homing behavior and, for some species, the high degree of nesting site fidelity (Miller, 1997). However, some studies have found a few female loggerheads trying to nest away from their former nesting sites, with the difference being hundreds of kilometers in Australia (Limpus, 2008) and tens of kilometers in South Africa (Nel *et al.*, 2013). This shows that sea turtles have the potential to forge range extensions (Monsinjon *et al*., 2019) by compensating for the loss of current nesting sites (Fuentes *et al.*, 2013; Hawkes *et al.*, 2009) with providing other suitable nesting beaches that are still available (Katselidis *et al.*, 2012; Pike, 2013).

5. Conclusions

The nesting beaches of loggerhead turtles occupy only a fraction of the available bioclimatic niche in tropical and subtropical coastal areas of the world and show evidence of bioclimatic imbalance. The niches in different oceanic regions are different, but there is no evidence of niche divergence. Differences in realized niches seem to be due to differences in accessible environmental space. New records of sporadic nestings, or attempts, are reported in southern Brazil, and at least one record of successful hatching was recorded. The Southern Subtropical Shelf seems to present bioclimatic suitability for nestings equivalent to the lowest values observed in regular beaches in Brazil, but higher than many beaches around the world.

Acknowledgments

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Supplementary Material for: **Sporadic nestings of sea turtles in subtropical southern Brazil: is it a bioclimatic suitable nesting area for loggerhead sea turtles (*Caretta caretta*)?**

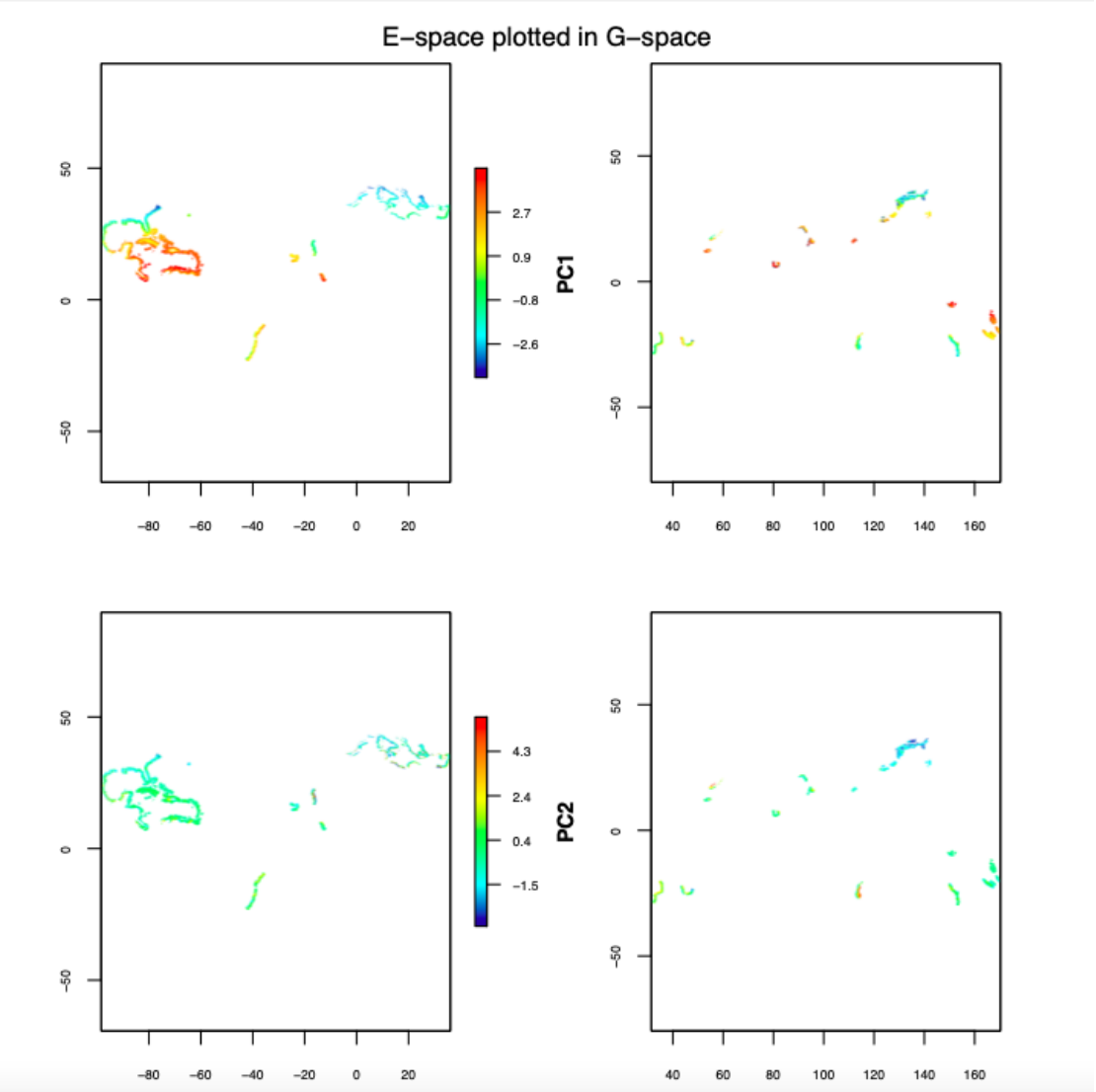


Fig. 1. Plots of E-space in G-space, determining how PC1 and PC2 are characterized in geographic space.

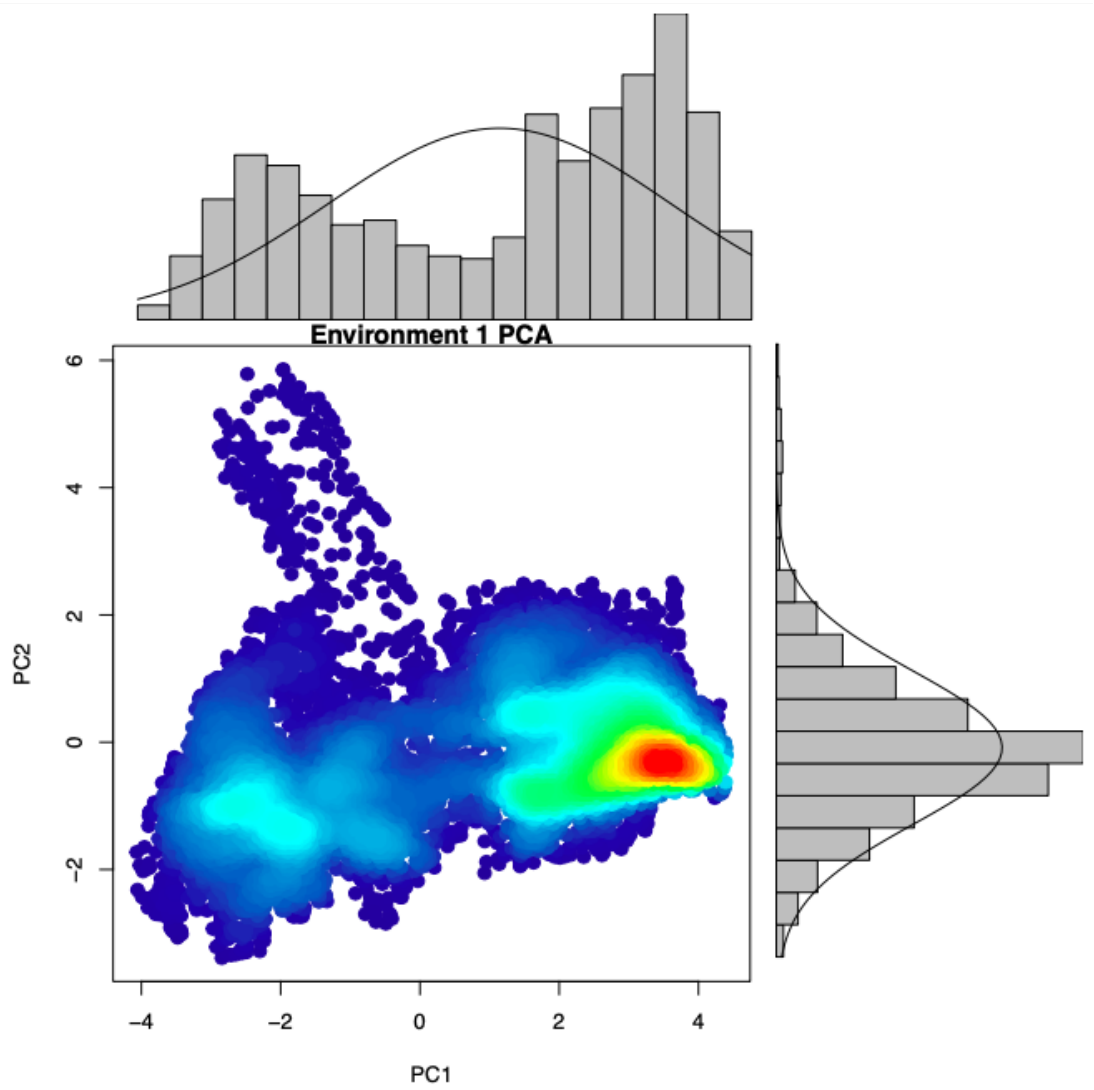


Fig. 2. A plot of raw data of population 1 (Atlantic-Mediterranean) and environment E-space. Cooler colors represent lower and warmer higher densities of E-space.

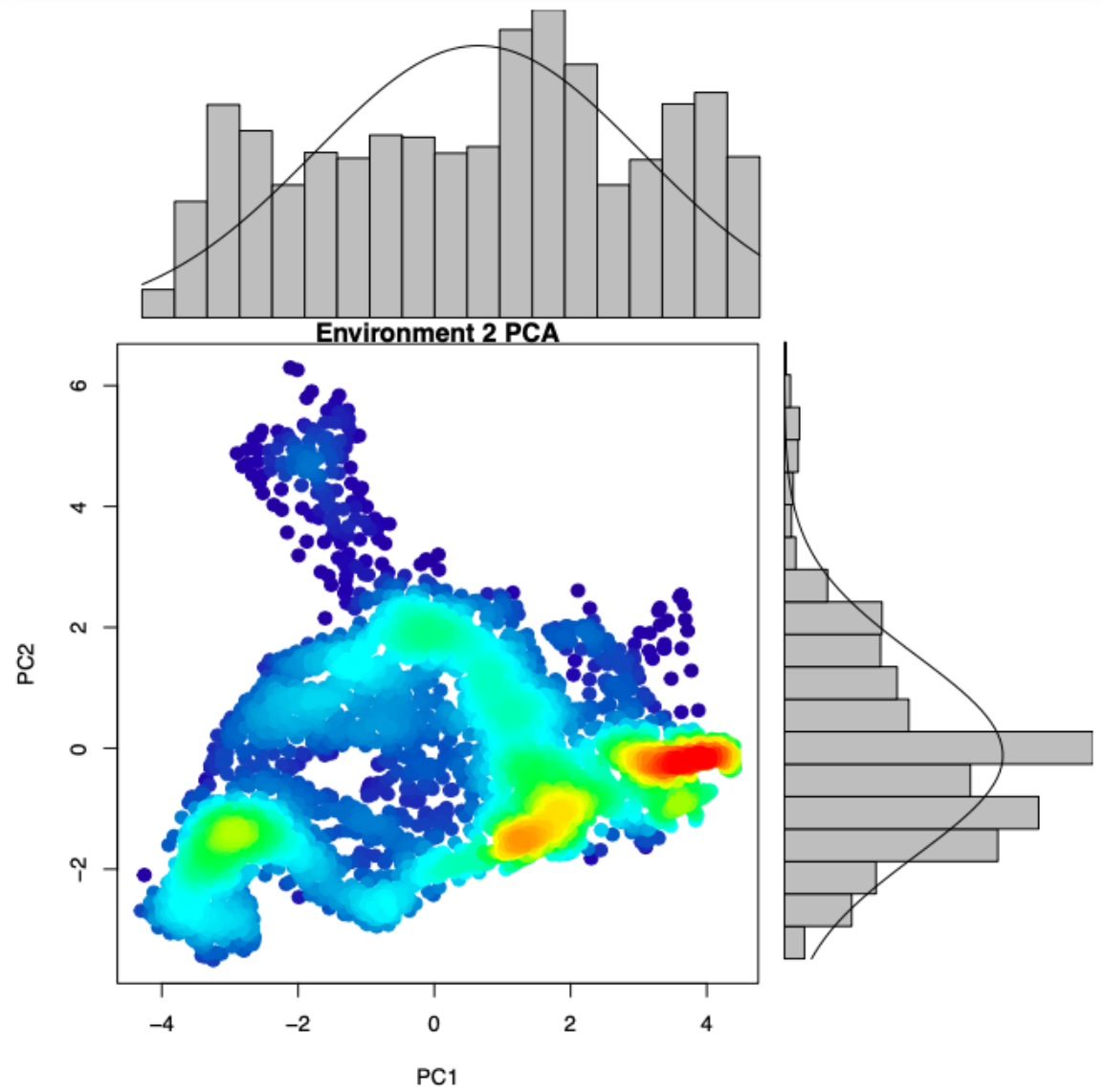


Fig. 3. A plot of raw data of population 2 (Indian-Pacific) and environment E-space. Cooler colors represent lower and warmer higher densities of E-space.

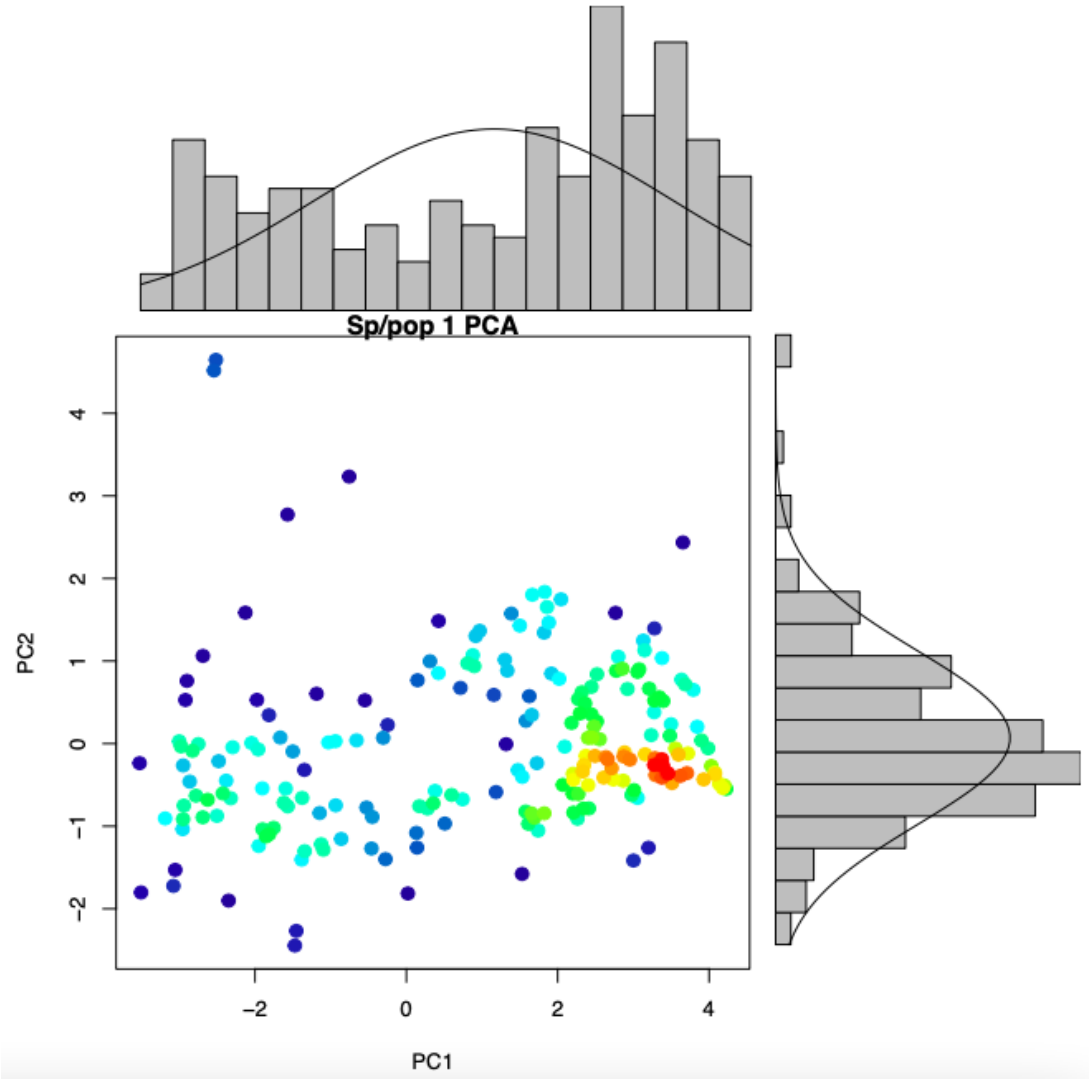


Fig. 4. A plot of raw data of localities occurrence for population 1 (Atlantic-Mediterranean).

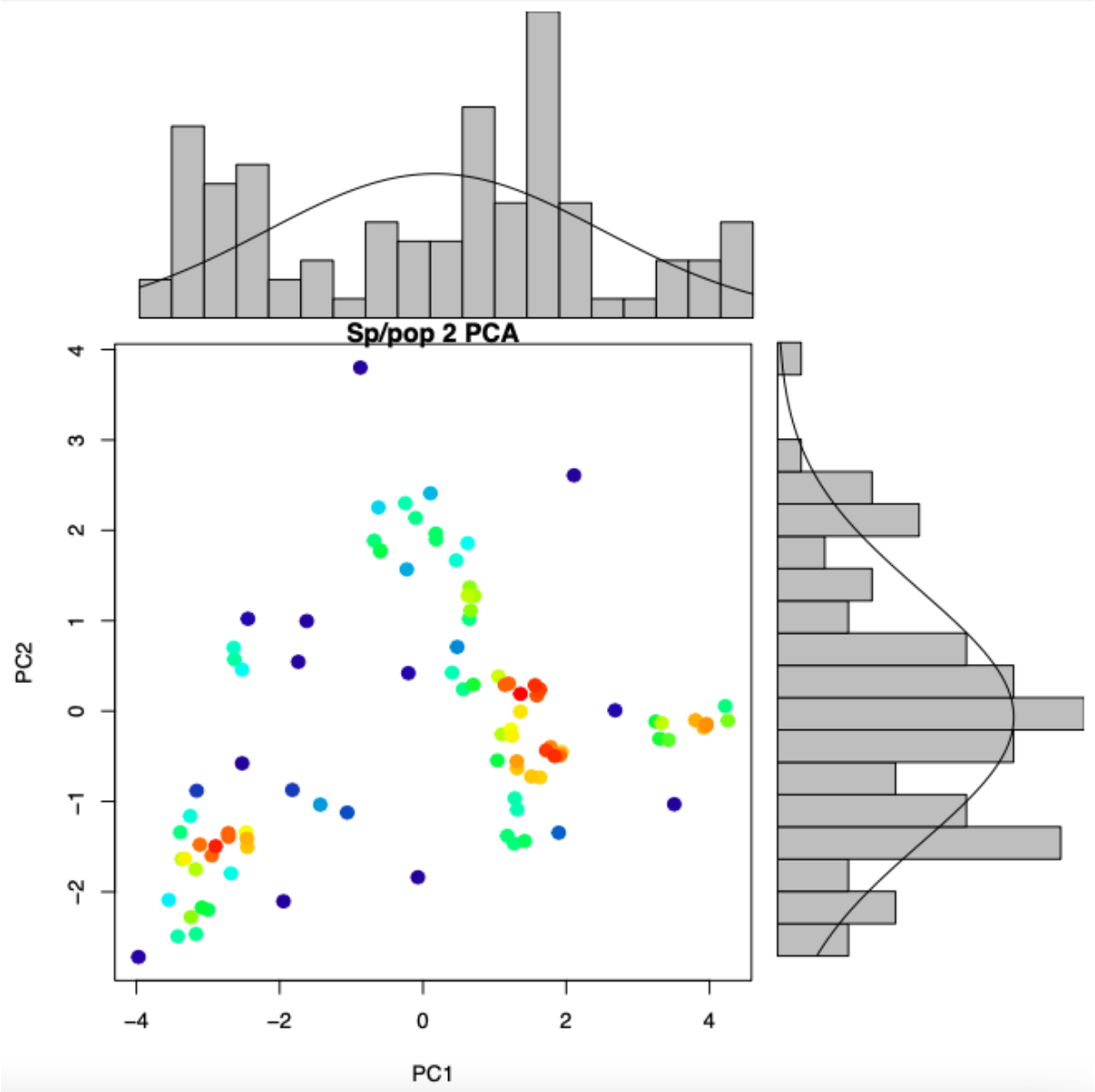


Fig. 5. A plot of raw data of localities occurrence for population 2 (Indian-Pacific).

CAPÍTULO III

Conclusões gerais

Conclusões

O presente estudo demonstrou que os nichos Atlântico-Mediterrâneo (população 1) e Índico-Pacífico (população 2) não são equivalentes. No entanto, ao realizar o Teste de Divergência de Nicho, não foram encontradas evidências de que eles tenham divergido e as diferenças podem ser resultado tanto do ambiente acessível como da biogeografia de suas regiões.

O nicho Atlântico-Mediterrâneo (população 1) tem a maior parte de sua ocupação na extrema direita da área de ambiente disponível, indicando que este nicho pode estar em desequilíbrio mais intenso se comparado com o Índico-Pacífico (população 2), onde há menor concentração em uma área específica.

Como não foram encontradas evidências de divergência de nicho, conclui-se que o melhor modelo para estimar a adequação bioclimática da distribuição das praias de nidificação é um modelo global.

Como esperado, as áreas de desova esporádica localizadas na Plataforma Subtropical Sul (SSS) apresentaram menor aptidão, sendo equivalente à menor aptidão para desova de tartaruga-cabeçuda no Brasil, mas ainda superior à aptidão de muitas desovas regulares áreas ao redor do mundo. As regiões do extremo sul do Brasil podem ser áreas importantes para continuar procurando nidificação esporádica e até mesmo para identificar a presença de supostas novas micropopulações.

Atualmente, não há um esforço de monitoramento voltado para esse objetivo, pois as ocorrências são muito raras. No entanto, o intenso monitoramento das praias hoje focado principalmente no registro de encalhes, aliado ao intenso esforço de diversas instituições científicas, tem permitido que as comunidades locais auxiliem cada vez mais nessas buscas.

Com números maiores de desova esporádica nos últimos anos, graças ao atual esforço de monitoramento das praias e ao aumento de relatos de moradores locais, infere-se que as áreas presentes na SSS podem se tornar mais importantes à medida que o aquecimento global as transforma em áreas mais adequadas que as áreas do norte do Brasil.

Infelizmente, a velocidade histórica de colonização das tartarugas marinhas é muito lenta e não deve ser capaz de responder às mudanças climáticas que ocorrem em escalas menores e mais rápidas, como em dezenas de anos. Em casos graves de perda de adequação,

propõe-se a migração assistida (ou colonização) de locais de nidificação por meio da movimentação de ovos para áreas mais adequadas, sendo a SSS uma região interessante para auxiliar na conservação de tartarugas marinhas.

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