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Fabiano Faga-Pacheco

Projeções futuras da distribuição de *Sargassum* (Fucales, Phaeophyceae) no Oceano Atlântico Ocidental em diferentes cenários de mudanças climáticas

Florianópolis
2023

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Dissertação submetida ao Programa de Pós-Graduação em Ecologia da Universidade Federal de Santa Catarina como requisito parcial para a obtenção do título de Mestre em Ecologia.

Orientador(a): Prof. Dr. Carlos Frederico Deluqui Gurgel

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O presente trabalho em nível de Mestrado foi avaliado e aprovado, em 24 de outubro de 2022, pela banca examinadora composta pelos seguintes membros:

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ATA Nº 024/2022/PPGECO

Ata de sessão pública de apresentação e defesa de Dissertação de Mestrado de Fabiano Faga Pacheco.

Aos vinte e quatro dias do mês de outubro de dois mil e vinte e dois, às 14h00min, por videoconferência, foi realizada a sessão pública de apresentação e defesa da **Dissertação de Mestrado**, na Área de Concentração **Ecologia**, do mestrando **Fabiano Faga-Pacheco** como requisito final para obtenção do título de **MESTRE** em **ECOLOGIA**, de acordo com a **Portaria nº 024/2022/PPGECO**. A banca foi composta pelos seguintes professores: **Dr. Carlos Frederico Deluqui Gurgel – Instituto de Biodiversidade e Sustentabilidade/UFRJ (Orientador), Drª. Fernanda Thiesen Brum – UFPR (Membro Titular – Externo à UFSC) e Dr. Eduardo Luís Hettwer Giehl – ECZ/CFM/UFSC (Membro Titular - Interno à UFSC)**, sob a presidência do primeiro. A dissertação tem como título **Projeções futuras da distribuição de *Sargassum* (Fucales, Phaeophyceae) no Oceano Atlântico Ocidental em diferentes cenários de mudanças climáticas.**

Houve participação por meio de sistemas de interação áudio e vídeo em tempo real pelos seguintes professores: Dr. Carlos Frederico Deluqui Gurgel, Drª. Fernanda Thiesen Brum e Dr. Eduardo Luís Hettwer Giehl.

Com base no resultado da defesa, a banca examinadora propõe que seja:

[X] **Aprovado**, devendo a versão definitiva da tese ser entregue em **até 90 dias**.

[ ] **Reprovado**.

Às 17 horas e 40 minutos foi lavrada a presente ata e encerrada a sessão, que vai assinada pelo candidato e pela banca examinadora.

Florianópolis, 24 de Outubro de 2022.

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DEDICATÓRIA

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RESUMO

Mudanças climáticas estão alterando a biota da Terra. Alterações na fenologia, morfologia, diversidade genética e distribuição das espécies marinhas têm sido reportadas em escala regional e global. Uma das mais profundas mudanças no ambiente marinho refere-se à tropicalização de comunidades bentônicas temperadas, com estimativas de alterações futuras na distribuição de espécies devido às mudanças no clima. Entretanto, pouco ainda é conhecido sobre os impactos do aquecimento global em comunidades de macroalgas marinhas tropicais. Espécies bentônicas formadoras de dossel, como as algas pardas conhecidas como sargaços (gênero *Sargassum*), têm um papel importante em substratos consolidados, providenciando complexidade ambiental e abrigo para uma variedade de organismos. Apesar da grande importância pelos serviços ecossistêmicos proporcionados por estas algas, evidências de perdas significativas de hábitat e biomassa têm sido reportadas nos últimos anos. Para compreender como mudanças futuras nos preditores ambientais podem afetar a distribuição de espécies de sargaço ao longo do oceano Atlântico Ocidental, foram aplicados Modelos de Nicho Ecológico (MNE) para 12 espécies amplamente conhecidas. Um outro MNE foi calculado para uma espécie aqui chamada de *Sargassum* WA, que representa seis espécies morfologicamente definidas que se encontram em uma politomia em árvores filogenéticas recentes. Projeções de adequabilidade ambiental foram feitas para o presente e para os cenários, um mais realista ("Representative Concentration Pathway" - RCP 4.5) e um mais pessimista (RCP 8.5) do IPCC. Os resultados indicam mudanças na adequabilidade ambiental latitudinal para as espécies, variando de 0.5º a 8.1º em direção ao norte e entre 0º e 5.5º em direção ao sul. Seis espécies de *Sargassum* devem ter reduzidas a sua área adequada entre 10% e 80%, enquanto outras seis espécies devem ter sua área adequada aumentada entre 4% e 168%. De maneira geral, as alterações previstas apresentam um padrão predominante de aumento da adequabilidade ambiental em maiores latitudes ao longo do oceano Atlântico Ocidental para todas as espécies, bem como uma diminuição da área de adequabilidade em latitudes menores para metade das espécies. Esse padrão é consistente com uma esperada tropicalização de ambientes em latitudes temperadas. Essas mudanças podem produzir perdas consideráveis em serviços ecossistêmicos mantidos por bancos de *Sargassum*, em particular em menores latitudes. Os resultados realçam a necessidade de políticas de conservação e estratégicas de manejo de espécies bentônicas de *Sargassum*, a fim de evitar efeitos negativos de mudanças na adequabilidade dos hábitats.

Palavras-chave: ambiente marinho bentônico; aquecimento global; ecologia de algas; espécies bentônicas de *Sargassum;* modelagem de nicho ecológico; modelo de distribuição de espécies; mudanças climáticas; Oceano Atlântico Ocidental.

ABSTRACT

Climate changes have impacted phenology, morphology, genetic diversity and distribution of marine species at regional and global scales. One of the more pervasive changes in the marine environment refers to the tropicalization of temperate benthic communities. Recent climate warming has changed the global redistribution of marine species, whether by poleward pattern of expansions or regional contractions at lower latitude. However, the impacts of future global warming on tropical marine macroalgal communities have been underrepresented. *Sargassum* species are foundation species that play an important role for marine ecosystems by providing complexity and shelter for a wide range of other organisms. To understand how future changes in abiotic variables could affect the distribution of *Sargassum* species along the Western Atlantic Ocean, we applied Ecological Niche Models (ENM) for 12 widely recognized species. Another ENM, dubbed *Sargassum* WA, was calculated and represents 6 morphologically defined species that area likely to be lumped following recent phylogenetic data. We produced models from the present to contrasting representative concentration pathways scenarios (RCP 4.5 and 8.5) of future climate changes. Our results showed changes in niche suitability between 0.5º and 8.1º northward, and 0º and 5.5º southward. Six species are likely to reduce their suitability area from 10% to 80%, while other six species are likely to expand their suitability area from 4% to 168%. Overall, suitability area showed an increase at higher latitudes for most species but decrease in lower latitude for half of the species were observed. This pattern is consistent with the expected tropicalization of temperate latitudes following global warming. Such changes can produce considerable losses in ecosystem services provided by *Sargassum* beds, particularly in edge populations. Our findings highlight the need of *Sargassum* conservation policies and management strategies to avoid the negative effects of shifts in benthic *Sargassum* habitat suitability.

Keywords: algal ecology; benthic marine environment; ecological niche modelling; future climate change; global warming; *Sargassum;* species distribution model; Western Atlantic Ocean.

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INTRODUÇÃO

Mudanças climáticas devem alterar a distribuição, fenologia e até mesmo a expressão do fenótipo de diversas espécies (Barry *et al.* 1995, Parmesan 2006, Thompson *et al.* 2002, Wernberg *et al.* 2012, Wiens 2016, Yan *et al.* 2017). Um dos processos associados com as mudanças climáticas nos ambientes marinhos é o aquecimento global (Levitus et al. 2000, Helmuth et al. 2002, Muller et al. 2009). O aquecimento das águas promove a tropicalização de comunidades bentônicas em ambientes marinhos temperados, representada tanto pelo desaparecimento de espécies de águas mais frias de ecossistemas temperados (i.e., florestas de kelps; Wernberg *et al.* 2010, 2016, Vergés *et al.* 2014, Franco *et al.* 2018, Jonsson *et al.* 2018) quanto pela sua substituição por espécies de águas mais quentes, como corais e peixes tropicais (Lima *et al.* 2007, Harley *et al.* 2012, Vergés *et al.* 2014). Evidência deste fenômeno tem sido reportada em sistemas marinhos temperados de locais como Austrália oriental (Vergés *et al.* 2016), Austrália Ocidental (Zarco-Perello *et al.* 2017, 2021), Atlântico Ocidental (Filbee-Dexter *et al.* 2016), Canal da Mancha (Hawkins *et al.* 2003, Southward *et al.* 1995), Península Ibérica (Casado-Amezúa *et al.* 2019) e Japão (Tanaka *et al.* 2012). Entretanto, os efeitos do aquecimento global sobre ambientes marinhos tropicais permanecem pouco conhecidos (Kleyplas 2019).

O gênero *Sargassum* é o gênero de algas pardas mais conspícuo nos bentos do infralitoral em latitudes tropicais (Tsuda 1972, Wanders 1976, Connor & Adey 1977, Morrissey 1980). *Sargassum* é responsável pela formação de várias agregações de macroalgas (chamadas de florestas ou bancos de sargaço ou *"Sargassum* beds*"*) em ambientes costeiros tropicais e subtropicais (Guimaraens *et al.* 1994, Mafra Junior 2001, Pereira *et al.* 2006). Espécies de *Sargassum* atuam como espécies fundadoras, pioneiras, propiciando heterogeneidade ambiental, refúgio para diversos animais vertebrados e invertebrados bênticos e servindo de substrato para organismos epizoóticos e epifíticos (Earle 1969, Paula & Oliveira-Filho 1980, Farnham *et al.* 1981, Brayner-Barros *et al.* 2006, Raut *et al.* 2018). A heterogeneidade ambiental em substratos consolidados é ampliada pela grande complexidade estrutural tridimensional do talo de certas algas pardas, inclusive *Sargassum* (Airoldi *et al.* 2014).

Sargassum é um gênero multidiverso compreendendo 537 espécies descritas no mundo todo, das quais 356 são consideradas válidas (Guiry & Guiry 2020). *Sargassum* apresenta uma variação morfológica interespecífica e intraespecífica muito grande (Cordero 1981, Moreira & Suárez 2002, Schell *et al.* 2015, Dibner et al. 2021), levando à descrição de muitas espécies baseadas na morfologia (Mattio & Payri 2011). Entretanto, estudos de sistemática filogenética recentes mostraram que a diversidade atual de *Sargassum* parece ser ainda menor do que previamente considerada (Phillips & Fredericq 2000, Mattio *et al.* 2009, Yip *et al.* 2020). Por exemplo, revisões da flora de *Sargassum* do oceano Índico Ocidental (Ilhas Maurício e Reunião) reconheceu como válidos apenas 7 espécies entre as 44 anteriormente reportadas (Mattio *et al.* 2013). Outro estudo reconheceu apenas 6 morfotipos dos 41 anteriormente registrados para Cingapura (Yip *et al.* 2018). Revisões também encontraram uma menor diversidade real de *Sargassum* do que os registros históricos na Polinésia Francesa, Nova Caledônia e África do Sul, principalmente devido a identificações equivocadas e falta de delimitação clara interespecífica (Mattio *et al.* 2008, 2015, Mattio & Payri 2009).

No oceano Atlântico Ocidental, 24 espécies de *Sargassum* foram reportadas, sendo 22 espécies bênticas e 2 pelágicas, ocorrendo do Canadá ao sul do Brasil (Taylor 1969, Ugadim 1973, Richardson 1975, Paula 1988, Camacho *et al.* 2015, Wynne 2017, González-Nieto *et al.* 2020). Apesar de alguns esforços para compreender as dinâmicas das espécies pelágicas de *Sargassum*, bem como entender os fatos que influenciam a distribuição das marés marrom (por vezes chamadas de "marés douradas", Lapointe 1986, 1995, Brooks *et al.* 2018, Oviatt *et al.* 2019, Wang et al. 2019, Godínez-Ortega *et al.* 2021, Jouanno *et al.* 2021), nenhuma predição está disponível para descrever como as mudanças climáticas podem alterar a adequabilidade ambiental das espécies bênticas de *Sargassum* e, portanto, de como isso pode afetar a distribuição futura das espécies (mas veja Gouvêa *et al.* 2020).

Espécies de *Sargassum* são sensíveis a impactos locais (como poluição), regionais (como desenvolvimento urbano) e globais (Dawes & Tomasko 1988, Steen 2004, Engelen *et al.* 2005, Miki *et al.* 2016, Abe *et al.* 2020). *Sargassum* pode também atuar como espécies bioindicadoras de efluentes industriais enriquecidos com nutrientes e de poluição por metais pesados, sendo capazes de sequestrar e acumular metais como cádmio, zinco e arsênio (Alquezar *et al.* 2013, Guitouni *et al.* 2016, Ho & Bantoto-Kinamot 2021). A presença de bancos de *Sargassum* saudáveis em determinados recifes é um indicador da saúde de toda a comunidade bêntica (Vroom & Braun 2010, Eggertsen *et al.* 2017). Portanto, entender como as mudanças climáticas afetarão a adequabilidade ambiental de *Sargassum* é uma etapa crucial para dar suporte a políticas de manejo, não apenas para preservar e proteger bancos de macroalgas, mas também para a conservação de comunidades bentônicas marinhas como um todo (Filbee-Dexter 2020).

ESPÉCIES SELECIONADAS

Sargassum bermudense

Espécie descrita a partir de exemplares de Bermuda e Cuba (Grunow 1916:147). Ocorre apenas nesses locais e nos Estados Unidos (Flórida e um registro em Massachusetts), alguns poucos locais do Mar do Caribe (Antígua e Barbuda, Bahamas, Porto Rico) e na Venezuela (Suárez 2005, Suárez *et al.* 2015, CRIA 2018, GBIF 2020, Guiry & Guiry 2020).

Dentre a lista de espécies com as quais *S. bermudense* já foi confundida, encontra-se *S. lendigerum*, *S. vulgare*, *S. cymosum* e *S. acinarium* (Schneider 2003). A variedade *S. bermudense* var. *stagnale*, cujos ramos podem chegar a 2m, foi encontrada somente em Walsingham Pond, nas Bermudas (Schneider 2003).

Sargassum buxifolium

Espécie descrita como variedade de *S. hystrix* por Chauvin em J. Agardh (1848:322). Foi elevado a espécie apenas recentemente (Wynne, 2011), baseado em diferenciações morfológicas em águas cubanas (Moreira & Cabrera 2007). A ocorrência da espécie está restrita à costa atlântica dos Estados Unidos (Massachusetts a Flórida), México, Belize e Caribe, chegando a águas sul-americanas na Colômbia e Venezuela (Earle 1969, GBIF 2020, Guiry & Guiry 2020). No Brasil, foi registrada em Fernando de Noronha e Abrolhos, no que parece ser o limite austral conhecido de sua distribuição (Figueiredo 2006, Oliveira *et al.* 2009).

Sargassum cymosum

O holótipo da espécie vem de águas brasileiras (C. Agardh, 1821). É a única espécie daqui selecionada que apresenta distribuição natural conhecida além do Atlântico. No Atlântico Ocidental, a espécie foi registrada da Carolina do Norte ao Brasil (Paula 1988, Paula & Oliveira 1982, Leite *et al.* 2007, Rover 2014, Camacho *et al.* 2015, Guiry & Guiry 2020,). A espécie também foi mencionada no Atlântico Central, nas Canárias, Açores, Cabo Verde e Ilhas Savage (Gallardo *et al.* 2016, Guiry & Guiry 2020).

A ocorrência da espécie no Atlântico Oriental está sujeita a maiores investigações taxonômicas. C. Agardh (1821, p.20) citou a espécie para os mares de Serra Leoa, como uma forma de *S. cymosum*, a saber forma β *Latifolium*. Com base nessa descrição, a ocorrência de *S. cymosum* na costa oeste africana foi ampliada para Gâmbia e Gabão e replicada em listas de macroalgas locais (Price *et al.* 1978). O material analisado por C. Agardh para Serra Leoa foi reconhecido como *Sargassum cheirifolium* por Kützing (1849:613). De Toni (1895) colocou o material do Gabão como sinônimo de *Sargassum vulgare*, inclusive *S. cheirifolium* e *S. cymosum* f. *Latifolium*. Atualmente, entretanto, *S. vulgare* está com status taxonômico não resolvido (veja Prud'homme van Reine 2011). Já *S. cheirifolium* está considerado hoje como *S. cymosum* var. *esperi* (Guiry & Guiry 2020).

Na África do Sul e em Madagascar, ocorre a variedade *S. cymosum* var. *scabriusculum* (Mattio *et al.* 2015, Vieira *et al.* 2021). Em revisão das espécies de *Sargassum* para a costa sul-africana, Mattio *et al.* (2015) encontrou que as citações na literatura para *S. cymosum* var. *gueinzii* e *S. cymosum* var. *lendigerum* tratam-se, na verdade, de *Sargassum elegans.* Já as citações de *S. cymosum* f. *dichocarpa* referiam-se a *S. cymosum* var. *scabriusculum*.

Menções a ilhas Galápagos pela Charles Darwin Foundation não constam mais de sua página na internet. Menção a ocorrência na Índia, China e Vietnã vêm de catálogos, sem consulta ao material de herbário para atualização taxonômica (Sahoo *et al.* 2001, Nguyen *et al.* 2013, Phang *et al.* 2016). A presença da espécie nas Ilhas Andaman ainda é incerta. A citação proveio de um catálogo (Silva *et al.* 1996) e a espécie não foi reencontrada em estudos posteriores (Karthick *et al.* 2013). A ocorrência de *S. cymosum* nesses locais parece advir de equívocos de identificação e necessitam de mais estudos taxonômicos. Por fim, a forma *S. cymosum* f. *borbonica* é considerada endêmica da Ilha Reunião (Mattio *et al.* 2013).

Como a taxonomia da espécie está relativamente bem resolvida para o Atlântico Ocidental, optou-se por usar apenas os dados constantes das Américas para a geração dos modelos.

Sargassum filipendula

A espécie foi descrita para águas possivelmente do México (C. Agardh, 1824:300) e foi mencionada para o Atlântico Central (Canárias, Madeira e Ilhas Savage) e Ocidental (Guiry & Guiry 2020). Neste último, foi listado de Massachusetts até o Brasil, com limite sul em Santa Catarina, mais especificamente em Florianópolis, nas praias do Sambaqui e Canasvieiras (Fialho 2015, GBIF 2020, Guiry & Guiry 2020).

Menções para outros locais parecem advir de equívocos de identificação. Listas para o Atlântico Oriental mencionam Gabão, Gana e Mauritânia (Price *et al.* 1978:148, Marcot-Coqueugniot 1991, John *et al.* 2014:46). Em sua revisão de *Sargassum* para a África do Sul, Mattio *et al.* (2015) afirmou que nenhuma espécie similar foi coletada nesse país, sugerindo equívoco na identificação de exemplar do Cabo da Boa Esperança (GBIF 2020).

Menções a Sri Lanka, Mar da China, Indonésia e Malásia provém de catálogos (Phillips 1995, Silva *et al.* 1996, Atmadja & Prud'homme van Reine 2014, Phang *et al.* 2016) e exemplares de Tailândia, Seychelles e Índia (GBIF 2020) também parecem advir de equívocos prévios de identificação, situação similar à identificação fenotípica de exemplares da Arábia Saudita (Abdel-Kareem 2009, John & Al-Thani, 2014:366). Uma melhor identificação unindo taxonomia comparada e filogenética pode elucidar melhor a distribuição da espécie fora do Atlântico Ocidental. Entretanto, a presença dela em sua área de origem e os padrões que se desenham até agora que aliam processos evolutivos e oceanográficos nos asseguram uma robusta segurança nas áreas de ocorrência da espécie nas águas americanas.

Sargassum furcatum

Espécie descrita por Kützing (1843:362) para as Ilhas Virgens Americanas, no Caribe. A espécie foi encontrada em alguns outros países insulares, como Cuba, Antilhas Holandesas e Trinidad e Tobago, além da Venezuela e Brasil (Zayas *et al.* 2002, Solé & Pardo 2005, Menezes-Széchy & Paula 2010, Guiry & Guiry 2020). Segundo Robinson *et al.* (2012), a espécie parece estar expandindo a sua distribuição, tendo sido encontrada recentemente no México e na Costa Rica (Dreckmann 1996, Cabrera *et al.* 2019). No Brasil, foi listada apenas para Bahia, Rio de Janeiro e São Paulo (Széchy & Paula 2000, Oliveira *et al.* 2002), em localidades específicas como Baía de Todos os Santos (Marins *et al.* 2008, Nunes & Paula 2002), Região dos Lagos (Ornellas & Coutinho 1998, Pereira & Yoneshigue-Valentin 1999, Rocha 2003) e litoral norte de São Paulo, com limite austral em São Sebastião (Paula 1988, Siqueira 2012).

A espécie foi ainda encontrada no Atlântico Central, nas Canárias e Ilhas Savage (Haroun *et al.* 2002, Parente *et al.* 2000) e nas Ilhas Chafarinas, nos Marrocos (Flores-Moya & Conde 1998). A menção às Filipinas provém de catálogo (Silva *et al.* 1987) e provavelmente trata-se de erro de identificação.

A variedade *S. furcatum* var. *diversifolium* foi originalmente descrita como uma forma de *S. vulgare* por Grunow (1916:41) para as Ilhas Canárias, Açores e Madeira.

Sargassum hystrix

Espécie descrita para os bancos do Campeche, no México (J. Agardh 1847:7). Ocorre da Virgínia, Estados Unidos, até São Paulo, Brasil, incluindo Bermuda, América Central, Caribe, Colômbia e Venezuela (Camacho *et al.* 2015, GBIF 2020, Guiry & Guiry 2020). *S. hystrix* já foi encontrada a 137m de profundidade (Littler & Littler 2000)

As ocorrências mencionadas em catálogo para Senegal e Serra Leoa (John *et al.* 2004) foram consideradas duvidosas por Lawson & John (1987). A ocorrência na Indonésia provém de catálogo (Atmadja & Prud'homme van Reine 2014). Menção para o Mar Vermelho (Einav *at el.* 2021) advém de um trabalho sobre ecologia bacteriana em macroalgas do Egito e não de taxonomia (Salem *et al.* 2011). Essas ocorrências, juntamente com a identificação de material de Seychelles como *S. hystrix* var. *spinulosum*, provavelmente são equívocos de identificação.

Sargassum platycarpum

Espécie descrita originalmente para a Martinica (Montagne 1848:248), ocorre em latitudes mais próximas do Equador, sendo listada do México, Caribe e Bermuda até o Brasil, onde foi encontrada na Laje de Santos e Ilhas de Alcatrazes e Queimada Grande (Rocha-Jorge 2015, GBIF 2020, Guiry & Guiry 2020).

No Atlântico Central, foi encontrado na Ilha da Madeira (Ferreira *et al.* 2018) e está presente em catálogos para Canárias e Cabo Verde (Price *et al.* 1978, John et al. 2004). A despeito da fragilidade e potencialidades apresentadas por essas últimas publicações, há registros da espécie em Abrolhos e no Recife Sebastião Gomes, mais próximos à costa (Torrano-Silva & Oliveira 2013). Já a menção da espécie no Golfo Arábico (Abdel-Kareem 2009) parece advir de equívoco de identificação.

Sargassum polyceratium

Espécie descrita para Cuba (Montagne 1837:356) com ocorrência a partir da Carolina do Norte, passando por Flórida e Bermuda, pegando o Golfo do México, Caribe, Colômbia, Venezuela e Brasil, onde ocorre até São Paulo (Venekey *et al.* 2008, Camacho *et al.* 2015, GBIF 2020, Guiry & Guiry 2020).

Menções ao Mar da China, Turquia e Indonésia vem de catálogos (Taskin *et al.* 2008, Atmadja & Prud'homme van Reine 2014, Phang *et al.* 2016) e na Filipinas foram citados em dois locais (Silva *et al.* 1987). Não há exemplares desses países nos catálogos de herbários verificados para este trabalho e a ocorrência da espécie nesses locais sem a ajuda humana é improvável.

Sargassum pteropleuron

Espécie típica de águas quentes, descrita para as Bahamas (Grunow 1868:55) e com ocorrência restrita aos Estados Unidos (Carolina do Norte, Flórida, Louisiana, Texas), Bermuda, América Central (Belize, Panamá), Caribe e Venezuela (Earle 1969, Prince & O'Neal 1979, Dawes *et al.* 1988, Dawes 1989, Camacho *et al.* 2015, GBIF 2020, Guiry & Guiry 2020).

Menções a Visayas Central, Filipinas (Silva *et al.* 1987), provavelmente provêm de equívocos de identificação.

Sargassum ramifolium

Espécie descrita para águas brasileiras (Kützing 1843:362, 1861:10) com distribuição basicamente do Golfo do México e Caribe ao Brasil (GBIF 2020, Guiry & Guiry 2020). Ocorre da Flórida e Bermudas até Bombinhas, Santa Catarina (Littler & Littler 1997, Rosado-Espinosa 2012, Semidey *et al.* 2013, Silva 2010, Carneiro 2017, Ballantine *et al.* 2016, Menezes-Széchy & Paula 2010).

Menções à presença da espécie na Mauritânia, Senegal e Guiné-Bissau na África e às Ilhas Canárias parecem ser verdadeiras (Welten *et al.* 2002, John *et al.* 2003, 2004).

Assim como todas as espécies, apenas utilizamos para a criação dos nossos modelos, os dados provenientes da costa ocidental do Atlântico.

Sargassum rigidulum

Espécie descrita para o Brasil a partir de exemplares de Pernambuco e Rio de Janeiro (Kützing 1849:615). Ocorre dos Estados Unidos (Flórida) e México até Santa Catarina, Brasil (Vroman 1968, Carela 1977, Oliveira Filho 1977, Moreira & Cabrera 2007, Bernecker 2009, Menezes-Széchy & Paula 2010, GBIF 2020, Guiry & Guiry 2020).

O aspecto geral da espécie assemelha-se a *S. cymosum*, com quem tem sido, por vezes, confundida (Oliveira Filho 1977). Alguns registros de *S. cymosum* foram baseados em exemplares de *S. rigidulum*, como ocorreu na Colômbia (Diaz-

Pulido & Díaz-Ruíz 2003), Venezuela (Cordero 2016), Barbados (Wynne *et al.* 2014) e, aparentemente, em Cabo Verde (Gabriel & Fredericq 2019). Camacho et al. 2015, por sua vez, coloca a espécie como sinônimo-júnior de *S. cymosum*, algo ainda não corroborado por Guiry & Guiry (2020).

A citação da espécie para o Japão (Yoshida *et al.* 2015) provavelmente se trata de um equívoco de identificação.

Sargassum stenophyllum

Martius é listado no AlgaeBase (Guiry & Guiry 2020) como o descritor da espécie, em livro escrito entre 1828 e 1834 de sua viagem pelo Brasil entre 1817 e 1820 (Martius 1834:8-9). Entretanto, nesse mesmo volume, o autor indica como referência o volume 1 (“*Algae, Lichenes, Hepaticae*”) de sua “*Florae Brasiliensis*” (Martius, 1833:47). De fato, o primeiro livro contém uma descrição extremamente simples da espécie, porém com ilustração, enquanto a segunda obra contém uma descrição muito mais detalhada e precisa da espécie. Em ambos os casos, também foi mencionada a citação prévia de Mertens para *Fucus stenophyllus*, referente à espécie, embora sem explicitar a literatura de referência.

A espécie foi descrita a partir de exemplares do Rio de Janeiro (*“Provinciarum Sebastianopolitanae”*), Bahia e São Paulo. O holótipo mencionado em Silva *et al.* (1996) como sendo de São Sebastião não leva em conta o antigo nome da então Província de São Sebastião do Rio de Janeiro.

A espécie está presente em águas da Colômbia, Venezuela e Brasil, tendo sido encontrada no Ceará (Caucaia) e da Bahia até o Rio Grande do Sul, onde foi encontrada até a Lagoa do Imbé (Eston & Bussab 1990, Haddad & Chiaverini 2000, Tanaka 2004, Scherner *et al.* 2012, Almeida 2014, Camacho *et al.* 2015, Oliveira *et al.* 2015, Machado *et al.* 2015, CRIA 2018, Razzera 2018, GBIF 2020).

Grunow (1916:138) considerou a espécie uma variedade de *S. cymosum*, citando-a para Açores, Senegal e Tenerife (nas Ilhas Canárias), locais sem registros recentes nem exemplares da espécie. A citação da espécie para a Nova Caledônia (Phillips 1995) proveio de exemplares que seriam de *S. aquifolium* (Mattio & Payri 2009). Já a ocorrência na Austrália e Nova Zelândia veio de um catálogo em que não consta nenhum voucher (Bostock & Holland 2010) e cuja identificação baseouse em *S. stenophyllum* J. Agardh, considerado "*nomen illegitimun*" - a mesma identificação usada para os exemplares da Nova Caledônia, devendo, portanto, tratar-se também de exemplares de *S. aquifolium*. *S. stenopphyllum* J. Agardh é considerado hoje sinônimo heterotípico de *S. novae-hollandiae* (Silva *et al.* 1996).

Sargassum WA

Trabalhos recentes e em andamento usando dados moleculares registraram uma diversidade genética muito pequena ou mesmo inexistente entre algumas espécies de *Sargassum* que ocorrem no Atlântico. As filogenias geradas mostraram uma politomia entre as espécies *S. cymosum, S. filipendula, S. furcatum, S. hystrix, S. polyceratium* and *S. stenophyllum*, sugerindo que elas podem ser conspecíficas. Elas formam um clado não resolvido dentro de árvores filogenéticas de máxima parcimônia dentro do subgênero *Sargassum* (Camacho *et al.* 2015; B. Barros-Barreto, M. T. Szechy & V. Cassano, unpub. data; Figura S1). Os registros dessas seis espécies foram unidos para modelá-las conjuntamente como uma única espécie filogenética, aqui chamada *Sargassum* WA.

Algumas das espécies aqui do estudo não constam ainda de análises filogenéticas, então sua posição evolutiva ainda não está clara com base nas melhores evidências hoje disponíveis. *S. pteropleuron* e *S. platycarpum* são espécies-irmãs que estão num clado diferente das espécies que compõem *Sargassum* WA. Já *S. buxifolium* foi originalmente descrito como uma variedade de *S. hystrix* (J. Agardh 1848:322) e apenas filogenias bastante recentes demonstraram sua relação muito próxima às espécies de *Sargassum* WA, apontando também para serem conspecíficas (Yip *et al.* 2020). A proximidade morfológica entre *S. bermudense* e *S. cymosum* também já foi registrada (Schneider 2003, Schneider & Flook, 2017) e novos dados moleculares incluem ambas espécies na mesma politomia de *Sargassum* WA (González-Nieto *et al.* 2020). Dados moleculares de *S. rigidulum* e *S. ramifolium*, bem como de várias outras espécies do Atlântico Ocidental, permanecem ausentes em filogenias. *S. rigidulum* já foi confundido com *S. cymosum* (Oliveira Filho 1977, Diaz-Pulido & Díaz-Ruíz 2003, Wynne *et al.* 2014, Cordero 2016, Gabriel & Fredericq 2019) e *S. ramifolium* já foi considerado uma variedade de *S. cymosum* (Grunow 1916:141, Paula 1988). Dessa forma, existe uma alta possibilidade de que essas duas espécies venham a compor o complexo de espécies aqui considerado como *Sargassum* WA.

OBJETIVOS

O objetivo principal do estudo é testar se as mudanças climáticas globais, em especial o aquecimento dos oceanos, promoverá alterações na adequabilidade ambiental nas áreas de ocorrência de *Sargassum* bentônico no Atlântico ocidental em cenários futuros de aumento da concentração de dióxido de carbono atmosférico.

Mais especificamente, os objetivos deste trabalho são:

(1) Predizer as mudanças nas latitudes de adequabilidade ambiental de 13 espécies bentônicas de *Sargassum* (12 espécies morfológicas e 1 filogenética) do Atlântico ocidental nos cenários RCP 4.5 (cenário mais plausível) e RCP 8.5 (mais pessimista) do IPCC (2014);

(2) Estimar as alterações quantitativas e espaciais na área de adequabilidade das espécies selecionadas de *Sargassum* nos cenários RCP 4.5 e RCP 8.5.

Baseadas nessas premissas, elaboramos as seguintes hipóteses:

(1) Haverá um aumento da área de adequabilidade ambiental para as espécies em maiores latitudes nos cenários futuros em relação ao cenário presente;

(2) Haverá diminuição geral da área de adequabilidade ambiental das espécies de *Sargassum*, com redução da adequabilidade em locais mais próximos à Linha do Equador.

Adicionalmente, hipotetizamos que:

(3) Os efeitos de aumento da latitude e diminuição da área serão mais pronunciados no cenário RCP 8.5 do que no cenário RCP 4.5.

CAPÍTULO ÚNICO

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DISTRIBUTIONAL RANGE SHIFTS OF BENTHIC *SARGASSUM* SPECIES (PHAEOPHYCEAE: FUCALES) UNDER FUTURE CLIMATE CHANGES IN THE WESTERN ATLANTIC OCEAN

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Abstract

Climate changes have impacted phenology, morphology, genetic diversity and distribution of marine species at regional and global scales. One of the more pervasive changes in the marine environment refers to the tropicalization of temperate benthic communities. Recent climate warming has changed the global redistribution of marine species, whether by poleward pattern of expansions or regional contractions at lower latitude. However, the impacts of future global warming on tropical marine macroalgal communities have been underrepresented. *Sargassum* species are foundation species that play an important role for marine ecosystems by providing complexity and shelter for a wide range of other organisms. To understand how future changes in abiotic variables could affect the distribution of *Sargassum* species along the Western Atlantic Ocean, we applied Ecological Niche Models (ENM) for 12 widely recognized species. Another ENM, dubbed *Sargassum* WA, was calculated and represents 6 morphologically defined species that area likely to be lumped following recent phylogenetic data. We produced models from the present to contrasting representative concentration pathways scenarios (RCP 4.5 and 8.5) of future climate changes. Our results showed changes in niche suitability between 0.5° and 8.1° northward, and 0° and 5.5° southward. Six species are likely to reduce their suitability area from 10% to 80%, while other six species are likely to expand their suitability area from 4% to 168%. Overall, suitability area showed an increase at higher latitudes for most species but decrease in lower latitude for half of the species were observed. This pattern is consistent with the expected tropicalization of temperate latitudes following global warming. Such changes can produce considerable losses in ecosystem services provided by *Sargassum* beds, particularly in edge populations. Our findings highlight the need of *Sargassum* conservation policies and management strategies to avoid the negative effects of shifts in benthic *Sargassum* habitat suitability.

Keywords: algal ecology; benthic marine environment; ecological niche modelling; future climate change; global warming; *Sargassum;* species distribution model; Western Atlantic Ocean.

Introduction

Climate changes are expected to change the distribution, phenology and even the phenotypic expression of several species (Barry et al. 1995, Thompson et al. 2002, Parmesan 2006, Wernberg et al. 2012, Wiens 2016, Yan et al. 2017). One of the processes associated with climate change in the marine environment is global warming (Levitus et al. 2000, Helmuth et al. 2002, Muller et al. 2009). Warming waters promote the tropicalization of temperate marine benthic communities, which means the local disappearance of temperate species in temperate ecosystems (e.g. kelp forests; Wernberg et al. 2010, Vergés et al. 2014, Wernberg et al. 2016, Franco et al. 2018, Jonsson et al. 2018) and their replacement by tropical species (e.g., corals, tropical fishes, Lima et al. 2007, Harley et al. 2012, Vergés et al. 2014). Evidence of this phenomenon has already been reported in temperate marine systems such as Eastern Australia (Vergés et al. 2016), Western Australia (Zarco-Perello et al. 2017, 2021), Western Atlantic (Filbee-Dexter et al. 2016), English Channel (Hawkins et al. 2003, Southward et al. 1995), Iberian Peninsula (Casado-Amezúa et al. 2019) and Japan (Tanaka et al. 2012). However, the effects of global warming on tropical marine environments remain poorly known (Kleyplas 2019).

The genus *Sargassum* is the most conspicuous subtidal benthic marine brown alga in tropical latitudes (Tsuda 1972, Wanders 1976, Connor and Adey 1977, Morrissey 1980). *Sargassum* is responsible for the formation of several seaweed forests (or *Sargassum* beds) in tropical and subtropical subtidal coastal environments (Guimaraens et al. 1994, Mafra Junior 2001, Pereira et al. 2006). *Sargassum* spp. act as foundations species, providing environmental heterogeneity, refuge for a range of benthic invertebrate and vertebrate animals and acting themselves as substrate for several epizootic and epiphytic taxa (Earle 1969, Paula & Oliveira-Filho 1980, Farnham et al. 1981, Brayner-Barros et al. 2006, Raut et al. 2018).

Environmental heterogeneity along hard-bottom substrates is increased by the greater structural three-dimensional complexity presented by some brown algal thalli, including *Sargassum* (Airoldi et al. 2014).

Sargassum is a very diverse genus, comprising 537 described species worldwide, of which 356 are considered valid (Guiry & Guiry 2020). *Sargassum* has extensive intra and interspecific morphological variation (Cordero 1981, Moreira and Suárez 2002, Schell et al. 2015, Dibner et al. 2021), leading to the description of many morphology-based species and infra-species taxa (Mattio and Payri 2011). However, recent molecular-based systematic studies have shown the actual species diversity to be smaller than previously appreciated (Mattio et al. 2009, Phillips and Fredericq 2000, Yip et al. 2020). For example, revisions of the *Sargassum* flora from western Indian Ocean (Mauritius and Réunion) merged 44 taxa into 7 taxonomically defined species (Mattio et al. 2013). Another study conducted in Singapore recognized only 6 morphotypes against 41 previously recorded species (Yip et al. 2018). Revisions also found a smaller *Sargassum* diversity than historical records at French Polynesia, New Caledonia and South Africa, mainly due to misidentifications and unclear species delimitation (Mattio et al. 2008, 2015, Mattio and Payri 2009, Mattio et al. 2015).

In the Western Atlantic Ocean, 24 *Sargassum* species are reported (22 benthic and 2 pelagic) from Canada to southern Brazil (Taylor 1969, Ugadim 1973, Richardson 1975, Paula 1988, Camacho et al. 2015, Wynne 2017, González-Nieto et al. 2020). Despite some efforts to understand the dynamics of pelagic *Sargassum*, as well as the factors influencing the distribution of “brown tides” or “golden tides” (Lapointe 1986, 1995, Brooks et al. 2018, Oviatt et al. 2019, Wang et al. 2019, Godínez-Ortega et al. 2021, Jouanno et al. 2021), no forecast is available describing how climate change might shift benthic *Sargassum*’s habitat suitability, and hence future species distributions (but see Gouvêa et al. 2020).

Sargassum species are sensitive to local (e.g., pollution), regional (e.g., urban development), and global (e.g. climate change) impacts (Dawes and Tomasko 1988, Steen 2004, Engelen et al. 2005, Miki et al. 2016, Abe et al. 2020). *Sargassum* species are bioindicators of nutrient-enriched industrial effluents and heavy metals pollution, being capable of sequestration of metals like cadmium, zinc and arsenic (Alquezar et al. 2013, Guitouni et al. 2016, Ho and Bantoto-Kinamot 2021). The presence of healthy *Sargassum* beds in a particular reef indicates the healthiness of the entire benthic community (Eggertsen et al. 2017, Vroom and Braun 2010). Therefore, to understand how climate change affects *Sargassum* suitability, in terms of extent and range, is a crucial step to support management policies not only to protect and preserve algal beds but also marine benthic communities in general (Filbee-Dexter 2020).

The main objective of this study is to test whether global climate change in the form of ocean warming under future CO_2 emission scenarios will promote changes in Western Atlantic benthic *Sargassum* suitability areas. We hypothesize that *Sargassum* spp. suitability areas will: (1) increase toward higher latitudes; and (2) reduce in Equatorial latitudes. To test these hypotheses, we produce niche distribution models (or habitat suitability models) to estimate present and future suitability habitat areas under future global warming scenarios for 12 of the most common benthic *Sargassum* morpho-species in the tropical Western Atlantic Ocean and for one phylogenetic-defined species formed by the merge of 6 morpho-species, following recently published and unpublished molecular datasets. We also expected that future changes in distribution and suitability area will be more pronounced in the worst-case RCP 8.5 scenario than in the RCP 4.5 lower emission scenario.

Materials and Methods

Delimited area

Western Atlantic (WA) ocean raster was created with QGIS version 3.4.2 software (QGIS Development Team 2018), extending from 70.34845º on the North to -58.14374º southwards between -102.9249º and -17.35459º longitudes. WA raster was used as a mask for the worldwide abiotic variable rasters. Raster cells without marine environments (i.e., island) were excluded. Only areas with minimum depth lower than 265 m were maintained, since it is the deepest known record of a macroalgae (Littler et al. 1985).

Sargassum *species*

We selected 12 of the 24 WA *Sargassum* species. The species were selected based on the following criteria: (i) the species must be described from WA specimens; (ii) the species must be restricted to the WA or almost all known specimens must be from WA waters; (iii) the species must inhabit benthic hard-bottom environments (pelagic and drifting taxa were excluded); (iv) the species must be morphologically distinguishable; (v) the species must have minimal taxonomy concerns, at least morphology-wise (see Prud'homme van Reine 2011). Additionally, the species needed to have at least 5 different occurrence records along the WA. The species selected under these criteria were: *S. bermudense, S. buxifolium, S. cymosum, S. filipendula, S. furcatum, S. hystrix, S. platycarpum, S. polyceratium, S. pteropleuron, S. ramifolium, S. rigidulum*, and *S. stenophyllum*. While there is still a debate underlying the boundaries between some Atlantic *Sargassum* species, recent published and unpublished molecular phylogenetic results reported very low to no genetic divergence between *S.*

cymosum, S. filipendula, S. furcatum, S. hystrix, S. polyceratium and *S. stenophyllum*, suggesting that they could be conspecific. They form an unresolved clade in maximum likelihood *Sargassum* subgenus *Sargassum* trees (Camacho et al. 2015; B. Barros-Barreto, M. T. Szechy & V. Cassano, unpub. data; Figure S1). Consequently, we also produced ecological niche modeling for a putative single species comprising the records of these six *Sargassum* species, herein named *Sargassum* WA.

Occurrence data

We searched for *Sargassum* species occurrence data in the Global Biodiversity Information Facility (GBIF, 2020), the speciesLink Network (CRIA 2018), references listed by AlgaeBase (Guiry and Guiry 2020), herbaria websites, and data provided by peer-reviewed indexed articles. Grey literature was also checked, including monographs, and annals of congress. For species with small sample sizes, we enhanced our literature survey effort to identify and assign correct coordinates. We excluded occurrence data without GPS coordinates and with coordinates in mainland or outside our study area, as well as probable misidentifications. With this dataset and WA raster, we remove duplicated coordinates, and only one occurrence per cell was considered. Detail of sorted species names, occurrence records and their latitudes and longitudes can be provided by request from the authors.

Environmental abiotic variables

We used abiotic variables rasters from Bio-ORACLE v.2.0 (Tyberghein et al. 2012; Assis et al. 2017) assisted by the "*leaflet*" (Cheng at al. 2019) and "*smdpredictors*" (Bosch 2018) packages for R (R Core Team 2019). We follow three criteria to select variables. First, variables must be available in both present and future scenarios. Second, the variables must represent *Sargassum* biology and physiology needs, limits and constraints. Third, the correlation between the variables must be < 0.70 (see Figure S2). According to these criteria, we selected four variables: the minimum depth of the seafloor, maximum sea water temperature at minimum depth, mean sea water salinity at minimum depth, and mean sea ice thickness (see also Appendix S1).

Temperature is one of the main parameters that will change in climate change scenarios. Different studies ENMs with aquatic organisms show the importance of mean sea surface temperature (Jueterbock et al. 2013, Riul 2015, Jayathilake and Costello 2020), seabed temperature (Simon-Nutbrown et al. 2020), maximum and minimum sea surface temperature (Jueterbock et al. 2013, Riul 2015, Franco et al. 2018, Gouvêa et al. 2020, Jayathilake and Costello 2020, Prinz 2020), mean sea surface at summer and/or winter seasons (Assis et al. 2014, Martínez et al. 2018) and seasonal variation in sea surface temperatures (Sudo et al. 2019) to the models prediction. We choose only mean sea surface temperature between them for the following reasons: (i) our organisms are tropical perennial species; (ii) we take account for suitable areas where the species can be found, regardless their reproductive or germinative status; (iii) some *Sargassum* species are stenothermic (Earle 1969); and (iv) to avoid highly correlated variables in the delimited study area.

Salinity can also help to better understand the *Sargassum* distribution in the Atlantic Ocean. Some species are stenohaline and are not found nearby greater river discharges or mangroves (Earle 1969). For other macroalgae, salinity contributed for ENM models (Jueterbock et al. 2013, Sandman et al. 2013, Franco et al. 2018, Jonsson et al. 2018). Despite Assis et al. (2014) did not find any importance of salinity for the temperate Sargassaceae *Fucus vesiculosus*, minimum sea salinity met with *Sargassum horneri* important variables (Li et al. 2020), and salinity was an important variable for benthic *Sargassum* globally distribution (Gouvêa et al. 2020).

Depth is variable that will not significatively change over the century in the Atlantic basin. Despite this aspect, bathymetry contributed to ENM models of shallow-water organisms (Simon-Nutbrown et al. 2020), including other Sargassaceae (Sandman et al. 2013, Jonsson et al. 2018). Otherwise, some species with specific thermic requirements may find in tropical deeper waters adequate environmental conditions, with sites eventually serving as refugia and contributing for populations genetic connectivity (Graham et al. 2007, Davis et al 2021).

Ice cover and distance of glacier are parameters commonly used to predict Arctic and Antarctic macroalgae suitability areas (Jerosch et al. 2019, Assis et al. 2022). Ice affects light input to above waters and consequently, photosynthetic rates (Runcie and Riddle 2006). Also, the ice crystals formation may lead to greater mechanical cell wall damage, even causing cell rupture (Sun and Li 2003, Bayer-Giraldi et al. 2014).

Prediction scenarios

We choose the following scenarios to predict suitability areas of *Sargassum* species: (i) present scenario (data range from 2000 to 2016); (ii) Representative Concentration Pathway (RCP) 4.5, a realistic scenario of greenhouse emissions, for the year 2100; and (iii) RCP 8.5, a “business-as-usual” pessimistic scenario of high carbon dioxide atmospheric concentrations at 2100 (IPCC 2014).

Ecological niche modelling

We provided an ensemble of models for all 13 selected Sargassum species. For the species with more than 35 independent occurrence records, we provided an averaging ensemble of 11 modelling algorithms. For species with less than 35 records, we used the "leave-one-out-cross-validation approach" (see below). The species with >35 records were: *S. cymosum*, *S. filipendula, S. hystrix, S. polyceratium*, *S. platycarpum, S. pteropleuron*, and the *Sargassum* WA species described above (Table 1).

We used profile, regression and machine learning methods. We generated and ran ten times the following ENM algorithms for each morpho-species, plus the *Sargassum* WA species: generalized linear model (GLM; McCullagh and Nelder 1989), generalized additive model (GAM; Hastie and Tibshirani 1990), classification and regression trees (CART; Breiman et al. 1984), boosted regression trees (BRT; Friedman 2001), multivariate adaptive regression spline (MARS; Friedman 1991), random forests (RF; Breiman 2001), support vector machine (SVM; Vapnik 1995), artificial neural networks (ANN; Rosenblatt 1958), maximum entropy (Maxent; Phillips et al. 2006), maxlike (Royle et al. 2012), and bioclim (Busby 1991). Some ENM algorithms require presence and absence data, while other algorithms need presence and background coordinates. For both algorithm categories we provided pseudo-absences points as either absence or background data. Pseudo-absences represent points in geographical space where the species probably do not occur (Jayathilake and Costello 2020). We randomly set one group of pseudo-absences points into our study area in an equal number of occurrences registered for each species (Phillips et al. 2009). We visually checked the pseudo-absences points to make sure they were reasonable. Pseudo-absence coordinates for each species can be found in Supplementary Table S2.

As a result of our selection criteria, we were left with 4 environmental variables (see above) to fit the models. We utilized 75% of randomly selected presence and pseudo-absence points as train data, and the other 25% of the points for testing the models. This procedure was repeated for each algorithm, species, and scenario. After each model was generated, the “sdm” program automatically changed the points used for train and test (Naimi and Araujo 2016). To predict the models in present and futures scenarios, we use only models with Area Under Receiver Operating Characteristic Curve (ROC-AUC) ≥ 0.70 and true skill statistics (TSS) ≥ 0.60. The mean parameters of each algorithm for each species can be assessed in Supplementary Table S1. We used “sdm” package to identify the suitability limits that maximizes TSS for each model. TSS provide a good balance between sensitivity and specificity and is independent of species prevalence (Allouche et al. 2006). Each model, from each algorithm outputted a map that was binarized following the limit maximization of TSS of each model. Values above TSS maximization limits were considered suitable niche values for a particular species. Values below the TSS maximization limits were considered unsuitable habitats. An averaging ensemble map for current and future scenarios was built by summing all generated suitability maps. For the final ensemble, suitability areas were considered true for areas recognized as suitable in at least 50% of generated maps.

Species with small sample sizes

For species with less than 35 occurrence records, we modeled ecological niche using leave-one-out-cross-validation (LOOCV; “jackknife approach”) in the Maxent program, version 3.6 (Pearson et al. 2007, Shcheglovitova and Anderson 2013, see Table 1). This approach leads to more realistic analyses for species with small sample sizes. We used default parameters for convergence threshold (10^5), with random sample of 10000 background points to fit present environmental conditions and 500 iterations. We choose “crossvalidation” in “replicate run type”, using the number of occurrence records as the number of replicates. We binarized each map using T10 (fixed cumulative value 10 complementary log-log transformation threshold, which considers an omission rate of 10%) as a minimum value, following Pearson et al. (2007). An ensemble was then prepared using only the cells present in at least 50% of the maps (Buckley et al. 2011, Principe et al. 2021).

Analytical notes

We compared the maximum northward and southward latitudes and the total suitability areas for each species, the change in the area occupied (present and two future scenarios), and the overlapping between present and future scenarios in the ensemble maps. Non-parametric Spearman correlations were calculated between percentage change in suitability area and percentage changes in overlap area, as well as between percentual changes in suitability area and latitudinal variation.

All the analyses were done in R using the packages *dismo* (Hijmans et al. 2017), *plyr* (Wickham 2011), *rgeos* (Bivand and Rundel 2019), *raster* (Hijmans 2020), *rgdal* (Bivand et al. 2019), *sdm* (Naimi and Araujo 2016), *SDMTools* (VanDerWal et al. 2014) and *usdm* (Naimi et al. 2013). Complete scripts used in this study are available in Appendix S3.

Results

Changes in latitudinal limits

Latitudinal limits of all species increased southward 1.08º in average under the RCP 4.5 scenario (range: from 0.17˚ for *S. filipendula* and *Sargassum* WA to 4.08˚ for *S. buxifolium*) and 2.92º under the RCP 8.5 scenario (range: from 0.25˚ for *Sargassum* WA to 5.5˚ for *S. rigidulum*). The only exception was *S. furcatum* who did not change its current south latitudinal limit under the RCP 4.5 scenario (Table 2). Species with the highest values in terms of their southernmost latitude limits in the present day, like *S. bermudense*, *S. filipendula* and *S. polyceratium*, showed the smallest values of future change in southern latitudinal limits under both RCP scenarios (0.7˚ to 1.0˚ southward shifts) (Figure 1B).

Northern latitudinal limits of all species increased northward by 2.14º in average under the RCP 4.5 scenario (from 0.50˚ for *S. cymosum* to 5.42˚ for *S. bermudense*) and 4.24º under the RCP 8.5 scenario (range: 1.67˚ for *Sargassum hystrix* to 8.02˚ for *S. bermudense*), without exceptions (Table 2). Species with the highest values in northernmost latitude limits in the present day (*S. bermudense, S. filipendula, S. buxifolium* and *Sargassum* WA) showed the greatest values of northward changes in latitude distributional limits under both RCP scenarios (Figure 1A).

There was no correlation between change in suitability area and latitudinal range, except for northward variation in RCP 8.5 scenario (Spearman rank correlation: rho = 0.58, S = 152, df = 11, p = 0.02, Figure S3).

Changes in suitability area

We found two different groups of species, according to the magnitude of their change in area. For S. bermudense, S. filipendula, S. hystrix, S. platycarpum, S. polyceratium and S. pteropleuron the models suggest an increase in suitability area in both scenarios, RCP 4.5 from 4.2% to 188%, and RCP 8.5 from 9.7% to 167.8%, respectively (Table 2, Figure 1). However, for the other six species (S. buxifolium, S. cymosum, S. furcatum, S. ramifolium, S. rigidulum and S. stenophyllum) the models showed a reduction in suitability area in both scenarios, RCP 4.5 from -10.1 to -60.4%, and RCP 8.5 from -23.8% to -80.2%. Greater changes in future suitability areas were found for species with the smallest present-day predicted suitability areas (S. pteropleuron with + 167.8%, and S. stenophyllum with -80.2%, Figure 3). For Sargassum WA, we found an 1% increase in suitability area in RCP 4.5 scenario and a -13.1% decrease in RCP 8.5 prediction (Table 2, Figure S4).

Changes in overlap area

Species that increased their suitability area in future RCP scenarios are expected to maintain their current suitability area, with 100% overlap between present and futures scenarios (Table 2). Conversely, species which showed reductions in future suitability areas, also reduced in the same magnitude their overlap areas. A high positive correlation between areas of overlap and changes in suitability area between present and future scenarios were observed (Spearman rank correlation: RCP 4.5, rho = 0.92, S = 29.2, df = 11, $p < 0.001$; RCP 8.5, rho = 0.95, S = 17.9, df = 11, $p = 3x10^{-7}$). Reduction in overlap areas occurred mainly in the Caribbean region, despite an increase in their poleward range suitability.

Assessment metrics

The mean AUC for the test data ranged between 0.82 and 0.97 (Table 1). To compose the ensemble forecasting of the predictions, we excluded algorithms that do not run or fit well (AUC < 0.8). So, we don't consider Bioclim's predictions for *S. filipendula*, GAM's models for *S. platycarpum,* Bioclim, GAM, CART and MAXLIKE predictions for *S. pteropleuron* and Bioclim, GLM, ANN and MAXLIKE algorithms for *Sargassum* WA (see Table S1).

Predictors contributions

The most important abiotic variable for all species was maximum sea water temperature at minimum depth, which contribution varied between 56.1% (in *S. hystrix*) and 99.5% (in *S. bermudense*) for the models (Table 1). Temperature contributed for more than 90% of the models in *S. bermudense* and *S. buxifolium*. Temperature was followed by salinity, depth and ice cover. Mean annual salinity contribution ranged between 0.2% for *S. bermudense* to 36.2% for *S. furcatum*. For all species but *S. bermudense* and *S. buxifolium*, salinity contribution was greater than 5%. For seven species (*S. cymosum, S. filipendula, S. hystrix, S. platycarpum, S. polyceratium* and *S. petropleuron,* and *Sargassum* WA) depth contribution was greater than 5%. Mean sea ice thickness contribution ranged between 0%, for species modeled only with Maxent, to 10% for *Sargassum* WA. For *S. cymosum, S. filipendula, S. hystrix* and *S. platycarpum* and *Sargassum* WA, ice thickness contributed > 5%.

Discussion

Latitudinal patterns

Our niche distribution models predicted that all 12 tropical *Sargassum* morpho-species and also *Sargassum* WA will expand their potential distribution poleward in both north and southward directions. This prediction evidences the ongoing process of tropicalization of temperate marine benthic ecosystems which has already been observed in other parts of the world (Lima et al. 2007, Vérges et al. 2014, Thibaut et al. 2015, Vérges et al. 2016, Smale 2020). For example, local kelp and temperate *Sargassum* forests have been replaced by tropical Phaeophycean species, including dense tropical *Sargassum* beds, in southern Japan (Tanaka et al. 2012). Significant changes in community composition are well-documented in Western Australian warm temperate kelp communities after marine heat waves, with the decrease in the abundance and cover of temperate kelp and temperate animals' species, followed by their replacement by tropical species (Wernberg et al. 2016). Niche distribution models for a range of temperate seaweed species also forecast range contractions and further poleward shifts (Martínez et al. 2018). The absence of canopy-forming species in areas where dominant temperate species become absent are expected to be occupied by tropical canopy-forming species.

The shift poleward is greater in RCP 8.5 scenario than in RCP 4.5 for all species, following the observed pattern of other macroalgae (Martínez et al. 2018, Li et al. 2020, Prinz 2020, Simon-Nutbrown et al. 2020). For 10 of the 13 *Sargassum* species here studied, habitat suitabilities were forecasted to expand northward more than 3° of latitude under the RCP 8.5 scenario, while only 5 species had a southward expansion predicted for the same magnitude. Our results suggest that potential tropicalization of high latitude habitats due to poleward range shifts in *Sargassum* species distribution might be more prevalent in the Northern

Hemisphere. *S. bermudense*, for example, showed the highest predicted northward shift value of habitat suitability range (8.08º), which is equivalent to a potential 1700 km increase in its northward distributional range (i.e., from Cape Cod, Massachusetts, USA, to north Newfoundland, Canada). This prediction could appear extreme, however, a northward ranged shift of 593 km in ~50 years has already been reported for *Sargassum flavifolium* along Portugal's coastline (Lima et al. 2007).

Local and regional impacts caused by pollution, urbanization, heavy balneability use, and environmental degradation can reduce the abundance of *Sargassum* beds in lower latitudes (Barradas et al. 2022). Empirical evidence of local and regional *Sargassum* bed losses, particularly those associated to highly urbanized coastal areas along the Western Atlantic Ocean has been documented (Scherner et al. 2013). Gorman et al. (2020) for example, reported decline in *Sargassum* spp. cover in the order of 2.6% per year, in the last five decades across 48 sites along 1000 km of the subtropical Brazilian coast. An average total loss of 52% cover across sites was reported, ranging from 20% to 89% cover loss depending on the studied site. Loss of climate suitability overlap herein predicted for six *Sargassum* morpho-species and *Sargassum* WA, predicted to occur mostly in the Caribbean region, will probably be aggravated by local and regional stressors, inducing greater losses of niche overlap.

Suitability Area

Different from our initial expectations, not all *Sargassum* species will suffer future reduction in their suitability area under both RCP 4.5 and RCP 8.5 scenarios. Half of *Sargassum* species will increase their suitability areas, while the other half will decrease their suitability areas in tropical latitudes, mainly in Central America, Gulf of Mexico and Caribe. A similar pattern was observed for 5 out of 6 tropical to warm-temperate species evaluated in

Southwestern Atlantic by Riul (2015). In these cases, species may develop new or exacerbate ongoing disjunct distributions, potentially leading to a decrease in genetic connectivity between southern and northern populations and isolate or reduced populations raising extinction probability (*sensu* MacArthur and Wilson 1963).

Our results suggest *S. stenophyllum* will be the most negatively affected by future climate change (in both RCPs scenarios). *S. stenophyllum* has the second smallest predicted present day suitability area and model forecasts show future disjunct antitropical distributions. Under future RCPs scenarios, low latitude *S. stenophyllum populations* may find suitable environmental conditions only offshore, in deeper, possibly mesophotic, habitats. Compared to other Western Atlantic *Sargassum* species, *S. stenophyllum* has relatively slower growth rates (Paula and Eston 1987) which may jeopardize even further its occurrence in coastal tropical and equatorial latitudes under future climate scenarios.

Sargassum pteropleuron turned out to be the species with the smallest present day suitability area but showing the biggest expansion in future suitability area. *S. pteropleuron* more than doubled its suitability area under RCP 4.5 and RCP 8.5 scenarios. Interestingly, *S. pteropleuron* is the species with the smallest number of distributional records. Nowadays, *S. pteropleuron* is restricted to the Caribbean and North America coasts (Prince and O'Neal 1979, Díaz-Piferrer 1981, Camacho et al. 2015), despite being an eurythermal and euryhaline species (Earle 1969). *S. pteropleuron* along with his sister-species, *S. platycarpum,* are genetically distinct from the younger Sargassum WA clade and belong to an independent lineage that dispersed throughout Atlantic less than 1.5 Mya, after the closure of Panama Isthmus (Phillips and Fredericq 2000, Camacho et al. 2015, Yip et al. 2020).

Except for *Sargassum* WA, the RCP 8.5 scenario indicated larger changes in suitability area for all species than those observed under the RCP 4.5 scenario. Species with present day reduced suitability area are expected to lose more area under the RCP 8.5 scenario than under the RCP 4.5 scenario. Species that increase their suitability area, show further increase under the RCP 8.5 scenario. This pattern of continuous and proportional increased in suitability area as the atmospheric carbon dioxide concentration increase has been reported for other marine species, including phaeophycean (Sudo et al. 2019, Prinz 2020, Li et al. 2020, Simon-Nutbrown et al. 2020, Principe et al. 2021). For the phylogenetic species *Sargassum* WA, the 1% raise in suitability area at RCP 4.5 scenario and 13.1% reduction at RCP 8.5 are similar to predictions observed for the warm-temperate *Sargassum horneri* (Li et al. 2020). *S. horneri* projections made by 2100 show a 2.3% increase in suitability area at RCP 2.6 scenario followed by a 87.6% decrease at RCP 8.5 (Li et al. 2020). The *Sargassum* WA differences in both scenarios led us to think that a little enhance in seawater temperature may have a very discrete positive effect on the specie, but in RCP 8.5 scenario, the seawater temperature may be hotter than its physiological requirements for survival (see Bozinovic and Pörtner 2015).

According to recent phylogenetic studies, morphological data and classic taxonomy (Mattio and Payri 2011, Camacho *et al.* 2015, Yip *et al.* 2020), all species that show reduction in their suitability areas are included in *Sargassum* Subgenus *Sargassum* Section *Sargassum.* These species form a morphological complex with recent evolutionary origin (≤ 1 Mya) whose ancestors arrived recently, ~200-400 thousand years ago, in the Atlantic Ocean (Yip et al. 2020). These species simply might not yet be evolutionarily adapted to future warmer ocean conditions and must migrate towards the pole to find temperatures similar to present day conditions or be extinct (Wiens 2016).

Overlap

For all species herein studied, very little divergence between future suitability areas and the overlap areas were observed. *Sargassum* species that showed an increase in future suitability area will keep their current suitability area (as probably their current actual area of occurrence) and just add further range extensions poleward. A reduction in overlap areas was only observed in *Sargassum* species showing a decrease in their future suitability areas. The main pattern observed was the maintenance of the present species suitability area - entirely or partially - with a little enhancement of the suitability area toward the poles. Riul (2015) found a similar pattern only for one tropical Brazilian waters macroalga, *Dictyopteris jolyana*. The overlap areas for 5 subtropical or "warm-temperate species" (*Gelidium coarctatum, Ceramium brasiliense, Cryptonemia delicatula, Levringea brasiliensis* and *Plocamium brasiliense*) did not match their present suitable habitats and the local maintenance of some species will be only possible with spatially disjunct populations (Riul 2015).

Further advances in molecular and genetic techniques to improve species delimitation and phylogenetic resolution among putative *Sargassum* species within the *Sargassum* WA species complex will help us better forecast future scenarios for potentially different *Sargassum* species, subspecies, or phenotypes. To model *Sargassum* WA, we used only *Sargassum* species for which molecular data is available. Thus, our *Sargassum* WA species comprises data for only 6 WA species. Molecular data from Atlantic *Sargassum* morpho-species included or excluded in this study might turn out to belong to the *Sargassum* WA complex defined here. How this potential future inclusions will influence *Sargassum* WA model results remain unknown. For example, *S. buxifolium* was described as a variety of *S. hystrix* (J. Agardh 1848) and only very recently new phylogenetic data demonstrate their very close phylogenetic relationship, pointing towards conspecificity (Yip et al. 2020). The morphological proximity between *S. bermudense* and *S. cymosum* has been reported elsewhere (Schneider 2003, Schneider and Flook, 2017). Very recently, González-Nieto et al. (2020) using molecular techniques considered these two species into the same polytomy as *Sargassum* WA species. Molecular-based phylogenetic data for *S. rigidulum* and *S.*

ramifolium, including other Atlantic *Sargassum* species, remain absent. In the past, *S. rigidulum* has been confused with *S. cymosum* (Oliveira Filho 1977, Diaz-Pulido & Díaz-Ruíz 2003, Wynne et al. 2014, Cordero 2016, Gabriel & Fredericq 2019) and *S. ramifolium* was considered as a *S. cymosum* variety (Grunow 1916, Paula 1988). Therefore, there is a high likelihood that these two species might belong to the *Sargassum* WA species complex as well.

Research Limitations

Our work considers only 4 environmental variables that cover the entire study area for all considered scenarios. Other abiotic and climatic variables (e.g., specific nutrients and co-factors) could help improve the fit of our models but unfortunately data availability is spatially or temporarily limited, or non-existent. An environmental variable that could substantially enhance our predictions are the presence of hard substrata. Benthic *Sargassum* are stenoancyric species, only fixing their holdfast in consolidated subtract, like rocks, corals, and anthropogenic facilities, rarely on wood (Earle 1969). The main difference in our suitability area projected for the present in relation to the known occurrence are the presence of suitability areas in places with mud or sand substrata. A detailed raster with substrate information could exclude areas with only soft-bottom seabed. Nevertheless, shipwrecks and oil platforms may have led to a *Sargassum* colonization of these new available substrata.

An increase in the number of collections of species with few records (i.e., *S. bermudense*) and in undersampled locations can increase the number of occurrences, improving the output of the most sensitive algorithms. Likewise, advances in modeling, with new and better algorithms, will increase prediction accuracy. Other considerations for improving the models and the predictions are discussed in Appendix S2.

Management and Conservation Strategies

Our results highlight the possibility of tropical WA *Sargassum* becoming part of the macroalgal component in current temperate environments. The tropicalization of temperate communities may be more evident in the Northern Hemisphere, where tropical *Sargassum* showed greater latitudinal displacement. Also, northern boundaries of the present suitability habitats have a greater area with shallow waters than the southern boundaries.

Habitats today occupied by species showing future reduction in suitability areas (i.e., *S. cymosum, S. stenophyllum*, *S buxifolium)* may be occupied by other *Sargassum* species (i.e., *S. hystrix, S. polyceratium*). The impact of *Sargassum* species' replacement over the algal community is currently unknown and hard to be determined. Depending on the velocity of ocean warming, luxuriant *Sargassum* beds may be replaced by habitats of less structural complexity, such as barrens or turfs (Airoldi et al. 2014, Gorman et al. 2020). The importance of management policies, including Marine Protected Areas and local habitat restoration, may warrant species conservation (Gianni et al. 2013, Schneider and Flook 2017). Research focused on mapping, monitoring and conservation are needed and must be encouraged.

Conclusions

Our results on the effect of climate change on WA *Sargassum* species distributions showed us an increase in latitudinal range toward the poles for all 13 species here considered, with broader effects on RCP 8.5 scenario than in RCP 4.5. Considering that *Sargassum* spp represent foundation species, this suggests a move of tropical systems into warm temperate habitats at higher latitudes. Half of the species showed an increase in its suitability area, while the other half showed a reduction in suitability area. Whenever there was an increase in the suitability area, the future projection incorporated the entire suitability area predicted for the present scenario. Species with reduced suitability don't present a major shift in relation to the present distribution but show a decrease in the suitability of tropical regions. Attention should be paid to an eventual increase in the area of occurrence of *S. pteropleuron* and to a potential drastic reduction in the Tropical populations of *S. stenophyllum, S. cymosum* and *S. buxifolium*. Efforts for conservation and management initiatives of these species must be maintained and expanded.

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List of Tables (Legends)

Table 1. Number of records used to produce niche distribution model for *Sargassum* species, values for mean test Area Under Receiver Operating Characteristic Curve (ROC-AUC), true skill statistics (TSS), fixed cumulative value 10 complementary log-log transformation threshold (T10), and the percentual relative contribution of the parameters temperature, salinity, depth, and ice to the model. We used TSS for those species with more than 35 records, for whom we used an ensemble approach. T10 was used for the species with few registers modeled with leave-one-out-cross-validation approach in Maxent only. The redder a cell, the greater the variable importance to the final model for each species.

Table 2. Suitability area, maximum North latitude (Max Lat North), variations northward (ΔNorth), maximum South latitude (Max Lat South), variation southward (ΔSouth), and overlap area between suitability occurrence in present and future scenarios for 13 benthic *Sargassum* species from the Western Atlantic Ocean. The percentage of the area and overlap area has the present projected scenario as reference. Latitudinal parameters are in degrees.

Table 1. Number of records used to produce niche distribution model for *Sargassum* species, values for mean test Area Under Receiver Operating Characteristic Curve (ROC-AUC), true skill statistics (TSS), fixed cumulative value 10 complementary log-log transformation threshold (T10), and the percentual relative contribution of the parameters temperature, salinity, depth, and ice to the model. We used TSS for those species with more than 35 records, for whom we used an ensemble approach. T10 was used for the species with few registers modeled with leave-one-out-cross-validation approach in Maxent only. The redder a cell, the greater the variable importance to the final model for each species.

Species	**Records**	**Mean AUC (range)**	**Mean TSS/T10 (range)**	**Temperature**	**Salinity**	**Depth**	**Ice**
S. bermudense	10	0.83 (0.62 - 0.99)	0.36 (0.32 - 0.44)	99,5%	0,2%	0,1%	0,1%
S. buxifolium	21	0.86 (0.59 - 1.00)	0.33 (0.27 - 0.36)	95,0%	4,5%	0,2%	0,3%
S. cymosum	62	0.82 (0.78 - 0.85)	0.64 (0.61 - 0.67)	68,9%	14,0%	6,7%	6,2%
S. filipendula	183	0.86 (0.83 - 0.91)	0.69 (0.66 - 0.76)	66,4%	10,6%	11,1%	8,6%
S. furcatum	33	0.89 (0.70 - 1.00)	0.34 (0.31 - 0.35)	61,7%	36,2%	2,1%	0,0%
S. hystrix	142	0.83 (0.79 - 0.87)	0.66 (0.62 - 0.68)	56,2%	25,1%	6,8%	7,2%
S. platycarpum	43	0.85 (0.82 - 0.89)	0.71 (0.63 - 0.77)	62,1%	19,2%	8,1%	7,0%
S. polyceratium	90	0.90 (0.85 - 0.92)	0.76 (0.70 - 0.80)	61,3%	24,9%	5,3%	4,7%
S. pteropleuron	52	0.86 (0.84 - 0.89)	0.73 (0.65 - 0.77)	73,1%	12,3%	12,6%	1,2%
S. ramifolium	24	0.89 (0.70 - 1.00)	0.37 (0.33 - 0.40)	78,4%	21,4%	0,2%	0,0%
S. rigidulum	29	0.93 (0.74 - 1.00)	0.35 (0.31 - 0.37)	70,7%	26,3%	3,0%	0,0%
S. stenophyllum	29	0.97 (0.92 - 1.00)	0.17 (0.15 - 0.18)	61,6%	34,6%	3,8%	0,0%
Sargassum WA	404	0.86 (0.84 - 0.88)	0.63 (0.61 - 0.64)	59,8%	15,5%	5,1%	10,0%

Table 2. Suitability area, suitability area variation (ΔArea), maximum North latitude (Max Lat North), variations northward (ΔNorth), maximum South latitude (Max Lat South), variation southward (ΔSouth), and overlap area between suitability occurrence in present and future scenarios for 13 benthic *Sargassum* species from the Western Atlantic Ocean. The percentage of the area and overlap area has the present projected scenario as reference. Latitudinal parameters are in degrees.

Species	**Scenario**	**Suitability Area (km²)**	**ΔArea (%)**	**Max Lat North**	**ΔNorth**	**Max Lat South**	**ΔSouth**	**Overlap Area (km²)**	**Overlap Area (%)**
Sargassum bermudense	present	2225197	0	41.84118	0	-40.22967	0	2225197	100
	RCP 4.5	2341813	+ 5.4	47.25702	5.41584	-40.47963	-0.24996	2225197	100
	RCP 8.5	2533400	+ 13.9	49.92328	8.08210	-41.22951	-0.99984	2225197	100
Sargassum buxifolium	present	1678061	0	39.84148	0	-31.81428	0	1678061	100
	RCP 4.5	1507977	- 10.1	41.34126	1.49978	-35.89699	-4.08271	1482665	88.4
	RCP 8.5	743374	- 55.7	47.25702	7.41554	-36.89684	-5.08256	629083	37.5
Sargassum cymosum	present	2017188	0	41.35021	0	-36.81171	0	2017188	100
	RCP 4.5	1521753	- 24.6	41.85018	0.49997	-37.06169	-0.24998	1517677	75.2
	RCP 8.5	699781	- 54.0	44.93333	3.58312	-40.06151	-3.24980	673056	44.5
Sargassum filipendula	present	2082507	0	43.93339	0	-40.47815	0	2082507	100
	RCP 4.5	2169444	+ 4.2	47.76649	3.83310	-40.64481	-0.16666	2082507	100
	RCP 8.5	2284614	+ 9.7	50.09968	6.16629	-41.22810	-0.74995	2082507	100
Sargassum furcatum	present	1463296	0	37.75847	0	-33.14741	0	1463296	100
	RCP 4.5	1050691	- 28.2	40.59137	2.83290	-33.14741	0	1046927	71.5
	RCP 8.5	1057763	- 37.7	41.42458	3.66611	-34.51864	-1.37123	1045386	71.4
Sargassum hystrix	present	1612724	0	38.51705	0	-31.56202	0	1612724	100
	RCP 4.5	1763806	+ 9.4	39.35033	0.83328	-33.14526	-1.58324	1612724	100

	RCP 8.5	1858465	+ 15.2	40.18362	1.66657	-34.31186	-2.74984	1612724	100
Sargassum platycarpum	present	1503744	0	36.35052	0	-29.14551	0	1503744	100
	RCP 4.5	1696117	+ 12.8	38.68371	2.33319	-30.47876	-1.33325	1503744	100
	RCP 8.5	1826365	+ 21.5	39.76698	3.41646	-31.39537	-2.24986	1503744	100
Sargassum polyceratium	present	1313469	0	35.76722	0	-26.89564	0	1313469	100
	RCP 4.5	1607232	+ 22.4	37.68377	1.91655	-27.64560	-0.74996	1313469	100
	RCP 8.5	1721550	+ 31.1	38.93369	3.16647	-30.72874	-3.83310	1313469	100
Sargassum pteropleuron	present	663327	0	35.43391	0	-25.56239	0	663327	100
	RCP 4.5	1449037	+ 118.4	39.43366	3.99975	-26.56233	-0.99994	663327	100
	RCP 8.5	1776542	+ 167.8	40.10029	4.66638	-30.56209	-4.99970	663327	100
Sargassum ramifolium	present	1565947	0	39.34156	0	-31.39768	0	1565947	100
	RCP 4.5	1310462	- 16.3	40.75801	1.41645	-33.14741	-1.74973	1299848	83
	RCP 8.5	1030171	- 34.2	41.34126	1.99970	-34.31390	-2.91622	1001235	63.9
Sargassum rigidulum	present	1456138	0	40.59137	0	-31.39768	0	1456138	100
	RCP 4.5	1128950	- 22.5	41.42458	0.83321	-33.14741	-1.74973	1128087	77.5
	RCP 8.5	1109425	- 23.8	43.67423	3.08286	-36.89684	-5.49916	1102225	75.7
Sargassum stenophyllum	present	795816	0	39.42488	0	-32.23088	0	795816	100
	RCP 4.5	315013	- 60.4	40.17477	0.74989	-33.14741	-0.91653	305970	38.4
	RCP 8.5	157738	- 80.2	41.34126	1.91638	-36.23027	-3.99939	129060	18.5
Sargassum WA	present	1768857	0	42.43348	0	-37.64499	0	1768857	100
	RCP 4.5	1786798	+ 1.0	44.10005	1.66657	-37.81165	-0.16666	1768857	100
	RCP 8.5	1536880	- 13.1	48.76643	6.33295	-37.89497	-0.24998	1523227	86.1

List of Figures (Legends)

Figure 1. Relation between maximum latitude with suitability area in the present scenario for each Western Atlantic *Sargassum* species and the latitudinal variation predicted in our model results. Similar dots represent the same species in different projected scenarios. Leftmost dot represents the present scenario, the middle dot represents the RCP 4.5 scenario, and the far-right dot represents RCP 8.5 scenario. (A) North latitude. (B) South latitude.

Figure 2. Habitat suitability model projections for 12 *Sargassum* species. Red areas refer to the suitability areas while blue areas refer to unsuitability areas for present (A, D, G, J, M, P, S, V, Y, B1, E1, H1), RCP 4.5 (B, E, H, K, N, Q, T, W, Z, C1, F1, I1) and RCP 8.5 (C, F, I, L, O, R, U, X, A1, D1, G1, J1) scenarios. Species tested: *S. bermudense* (A-C), *S. buxifolium* (D-F), *S. cymosum* (G-I), *S. filipendula* (J-L), *S. furcatum* (M-O), *S. hystrix* (P-R), *S. platycarpum* (S-U), *S. polyceratium* (V-X), *S. pteropleuron* (Y-A1), *S. ramifolium* (B1-D1), *S. rigidulum* (E1-G1), and *S. stenophyllum* (H1-J1).

Figure 3. Changes of future suitability area for Western Atlantic *Sargassum* species. Similar dots represent the same species in different projected scenarios. Dashed line represents the projected suitability area for the present scenario. Dots on the left side of the line represent a decrease in suitability area. Dots on the right side highlight an increase in the suitability area. Dots on the dashed line show the present scenario for each species. Dots next to the dashed line show the RCP 4.5 scenario and points further away represent the RCP 8.5 scenario, with exception of *S. furcatum* whose most distant point represents the RCP 4.5 scenario, and *Sargassum* WA whose the dot on the right side of the dashed line represents RCP 4.5 scenario and the dot on the left side represent the RCP 8.5 scenario.

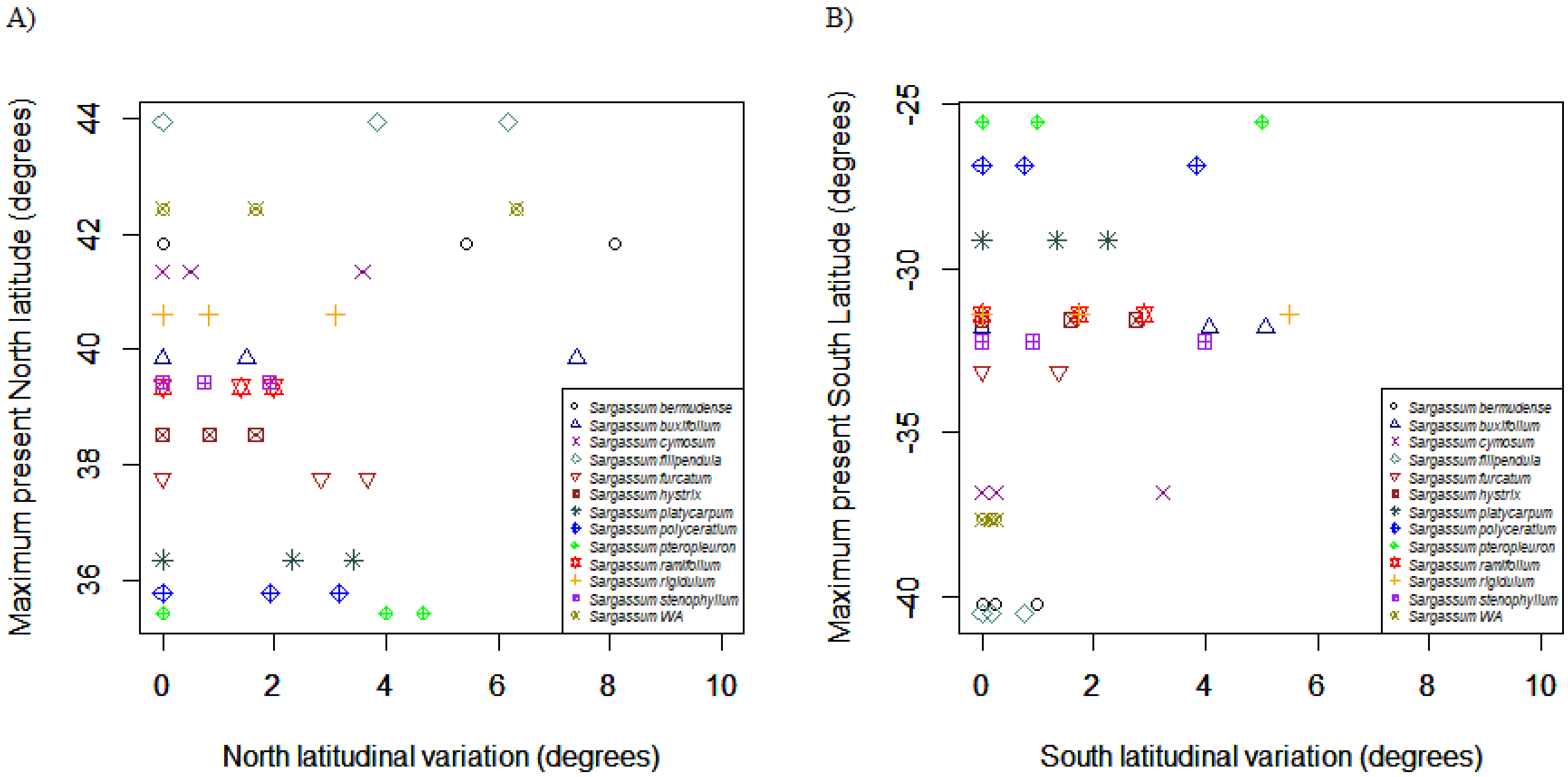
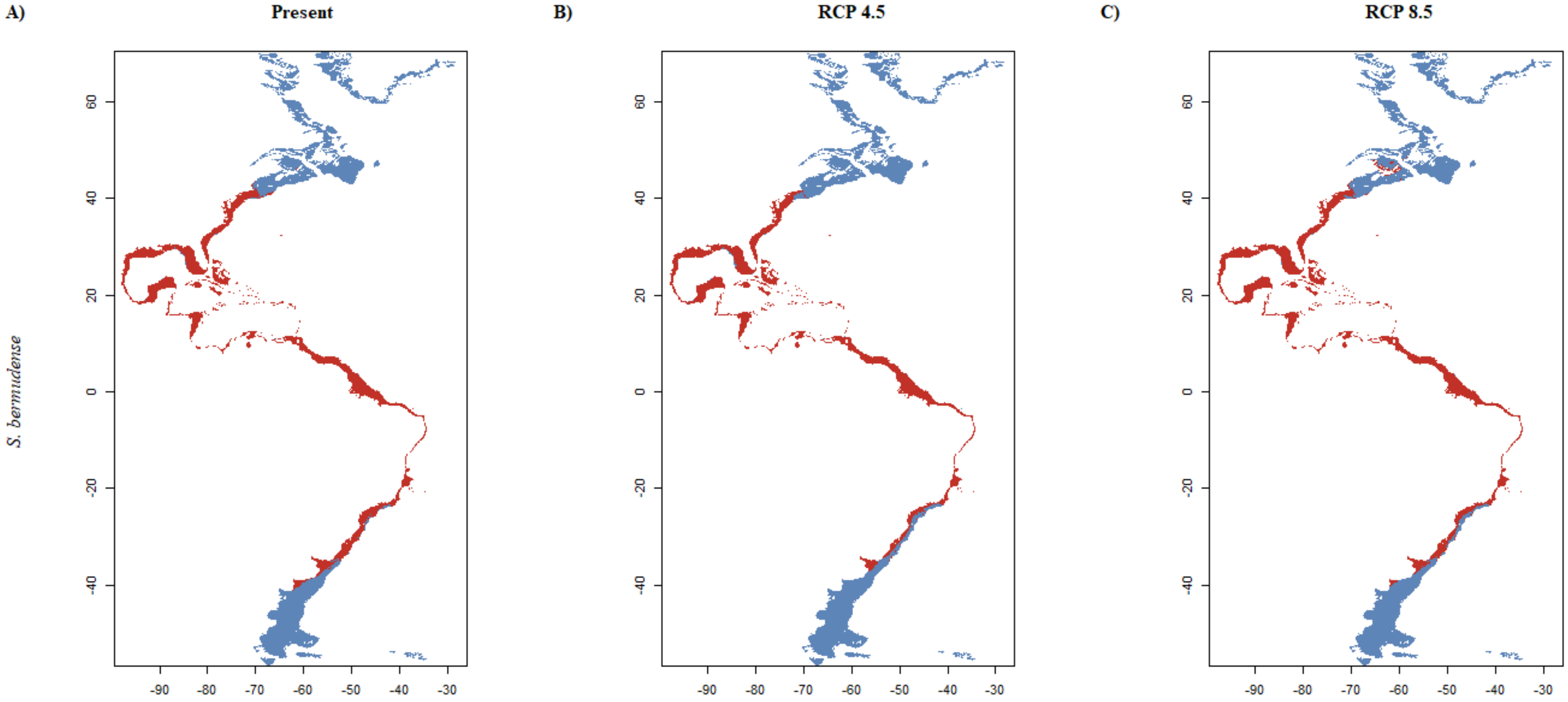
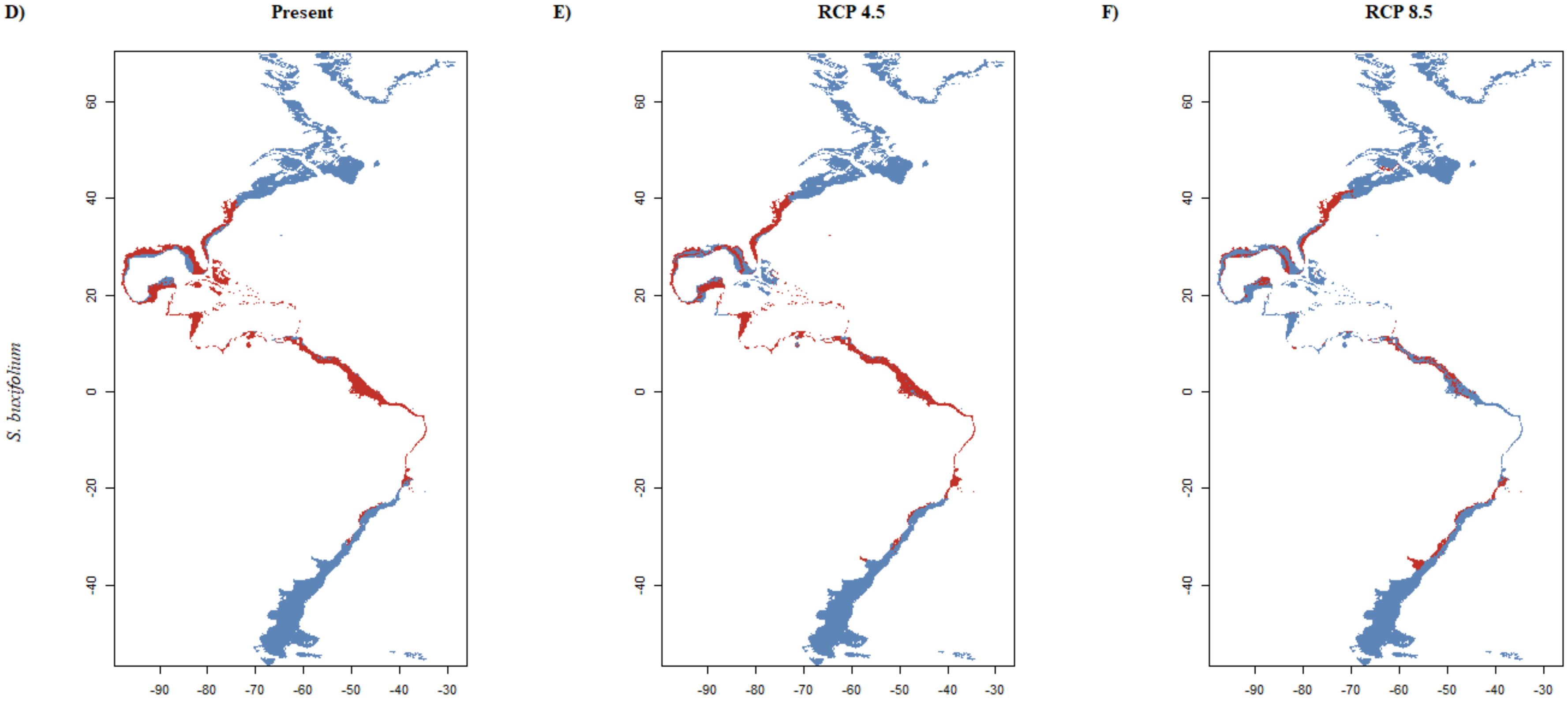
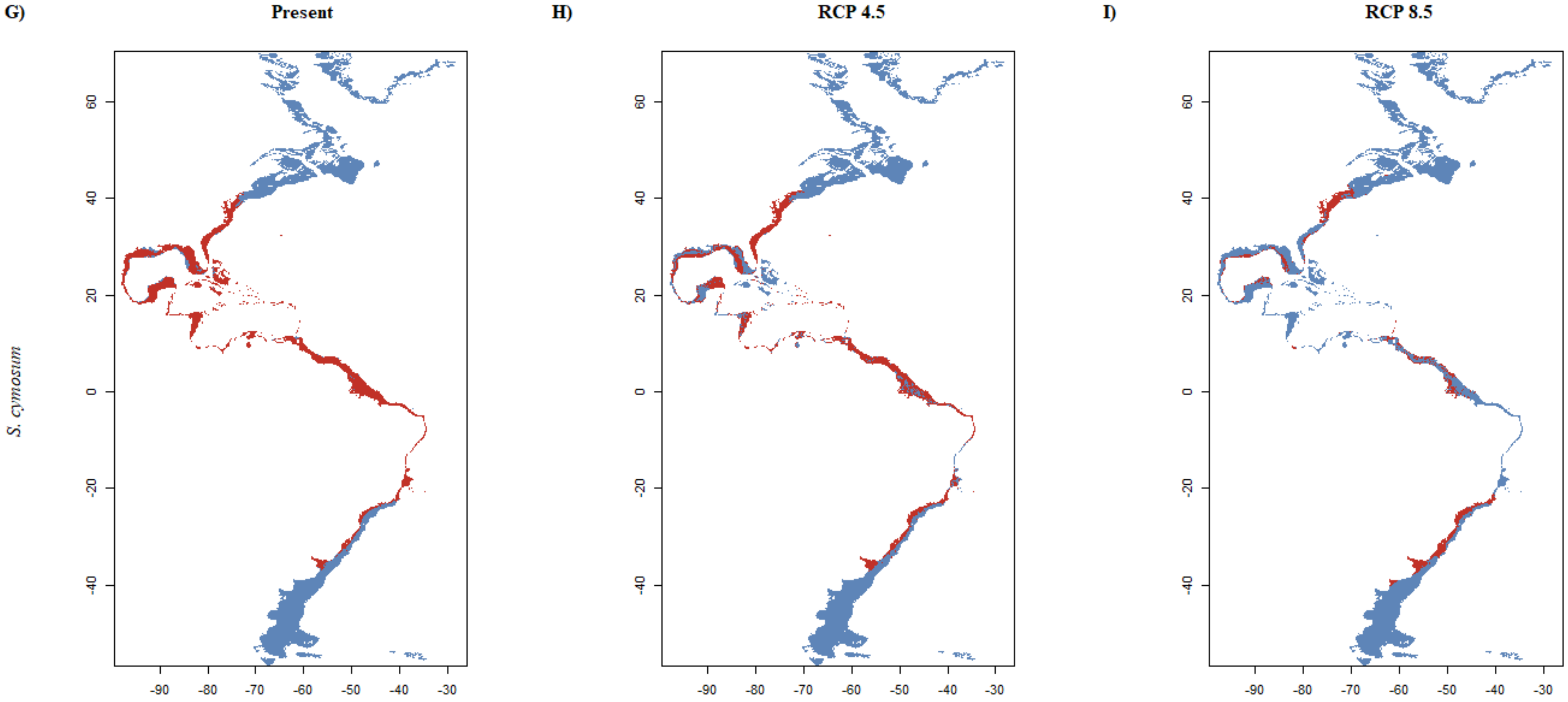


Figure 1. Relation between maximum latitude with suitability area in the present scenario for each Western Atlantic *Sargassum* species and the latitudinal variation predicted in our model results. Similar dots represent the same species in different projected scenarios. Leftmost dot represents the present scenario, the middle dot represents the RCP 4.5 scenario, and the far-right dot represents RCP 8.5 scenario. (A) North latitude. (B) South latitude.

Figure 2. Habitat suitability model projections for 12 Sargassum species. Red areas refer to the suitability areas while blue areas refer to unsuitability areas for present (A, D, G, J, M, P, S, V, Y, B1, E1, H1), RCP 4.5 (B, E, H, K, N, Q, T, W, Z, C1, F1, I1) and RCP 8.5 (C, F, I, L, O, R, U, X, A1, D1, G1, J1) scenarios. Species tested: *S. bermudense* (A-C), *S. buxifolium* (D-F), *S. cymosum* (G-I), *S. filipendula* (J-L), *S. furcatum* (M-O), *S. hystrix* (P-R), *S. platycarpum* (S-U), *S. polyceratium* (V-X), *S. pteropleuron* (Y-A1), *S. ramifolium* (B1-D1), *S. rigidulum* (E1-G1), and *S. stenophyllum* (H1-J1).

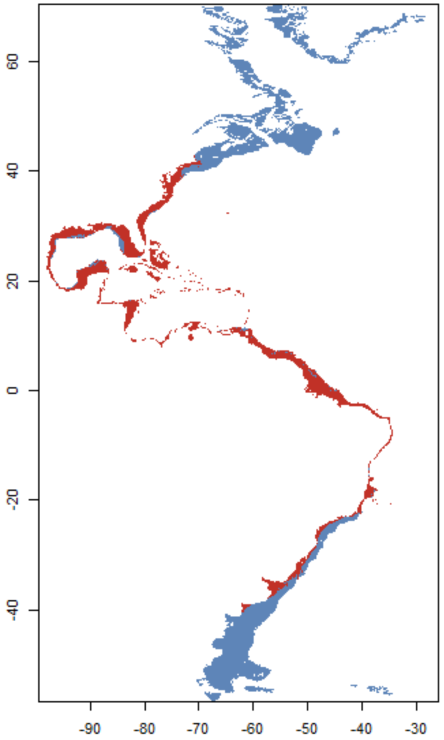

A)
Present
B)
RCP 4.5
C)
RCP 8.5
S. bermudense
60
40
20
0
-20
-40
-90
-80
-70
-60
-50
-40
-30


D)
Present
E)
RCP 4.5
F)
RCP 8.5
S. buxifolium
60
40
20
0
-20
-40
-90
-80
-70
-60
-50
-40
-30

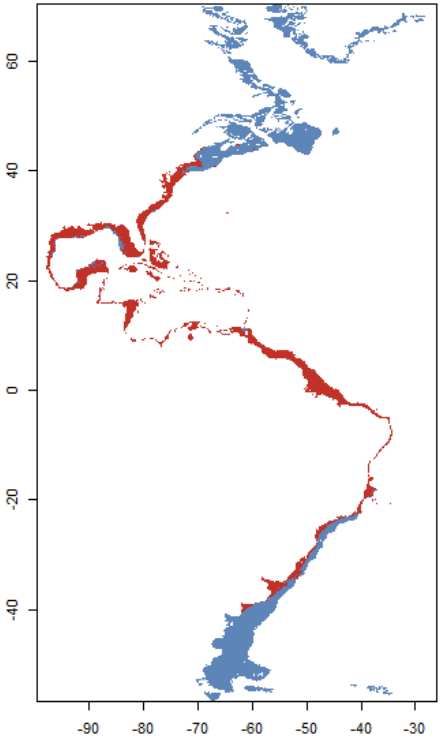

G)
Present
H)
RCP 4.5
I)
RCP 8.5
S. cymosum
60
40
20
0
-20
-40
-90
-80
-70
-60
-50
-40
-30

S. filipendula

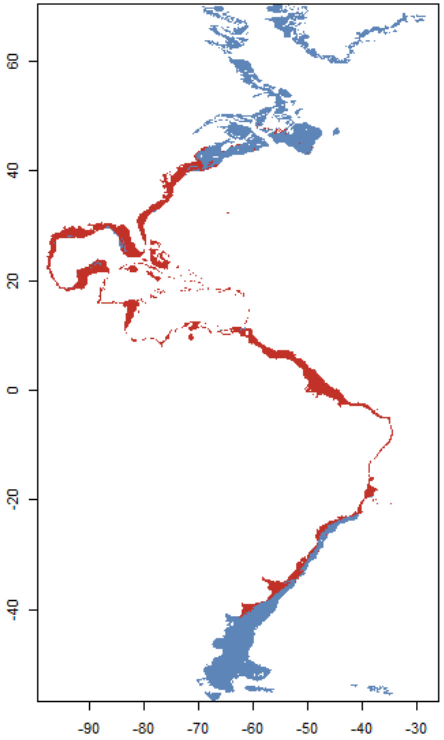
J) **Present**

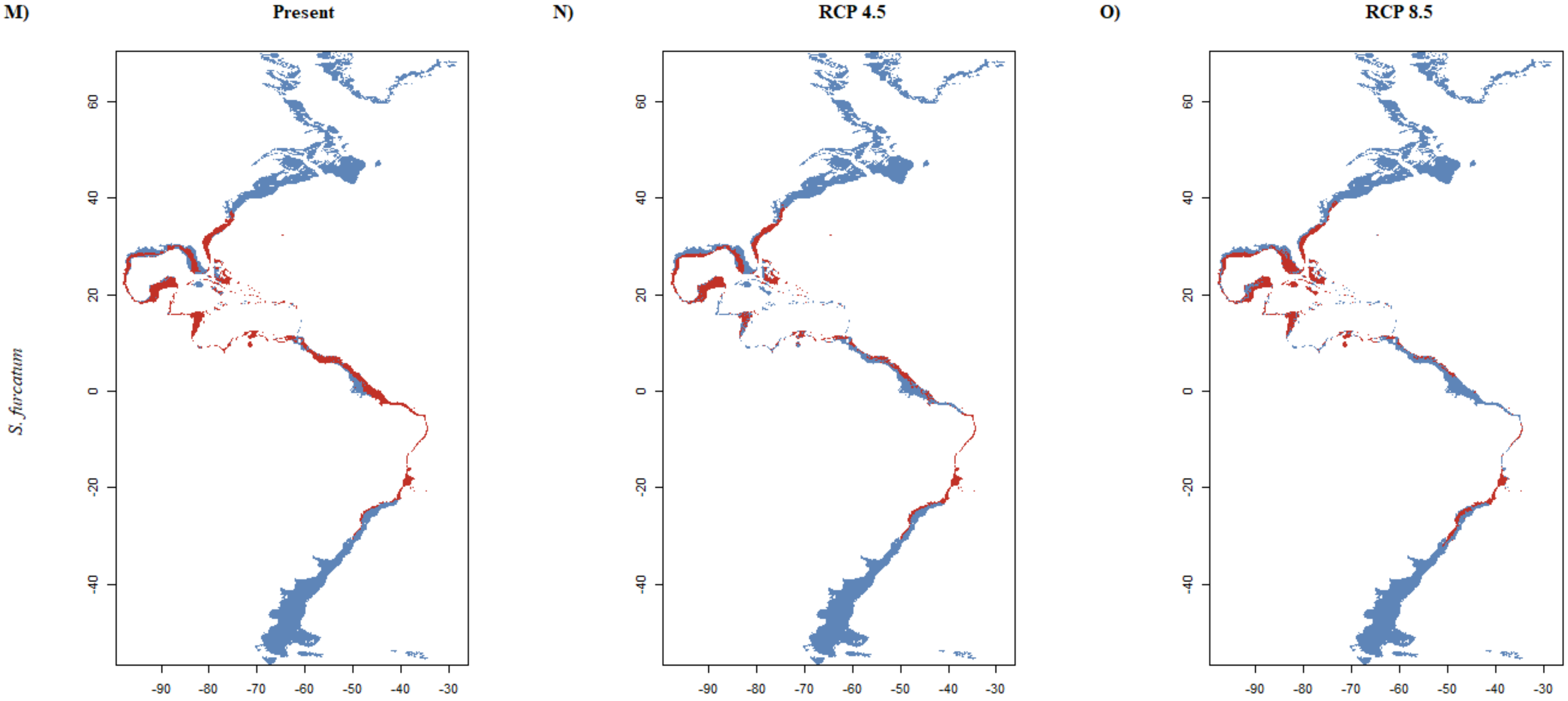


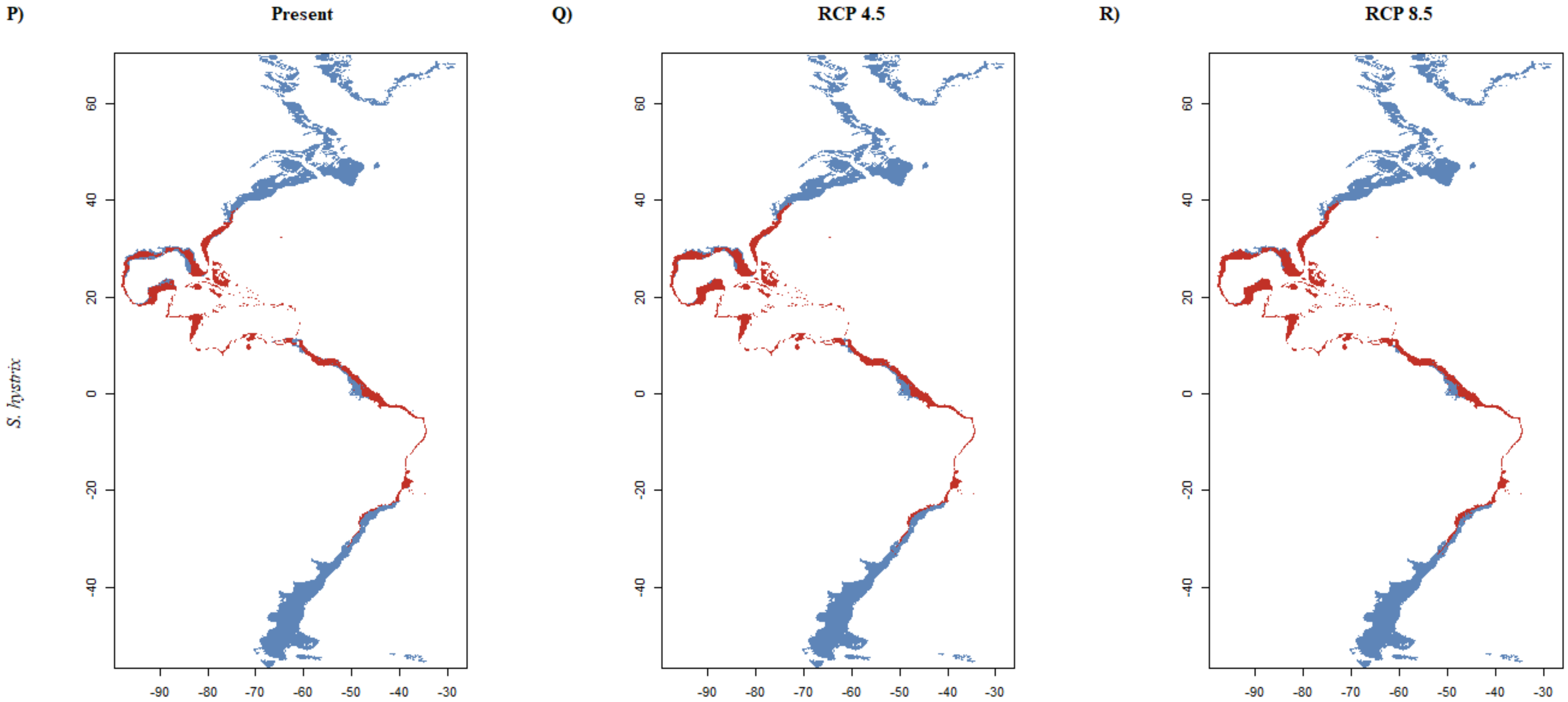
K) **RCP 4.5**



L) **RCP 8.5**

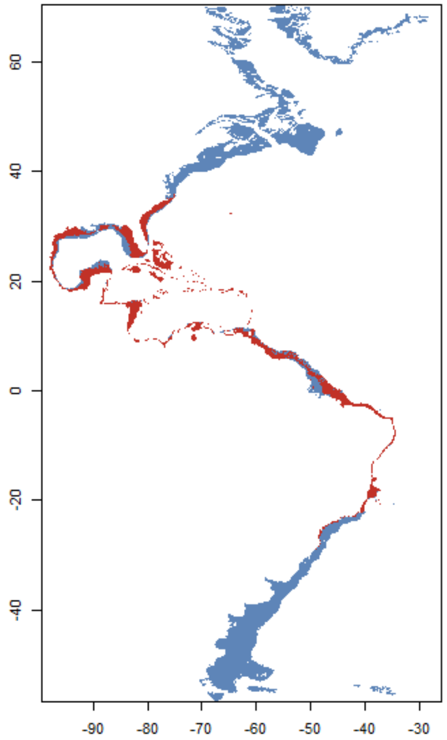



M)
Present
N)
RCP 4.5
O)
RCP 8.5
S. furcatum
60
40
20
0
-20
-40
-90
-80
-70
-60
-50
-40
-30

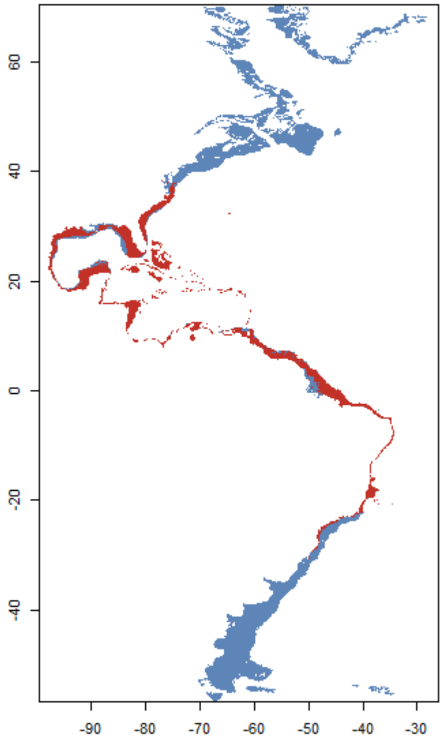

P)
Present
Q)
RCP 4.5
R)
RCP 8.5
S. hystrix
60
40
20
0
-20
-40
-90
-80
-70
-60
-50
-40
-30

S. platycarpum

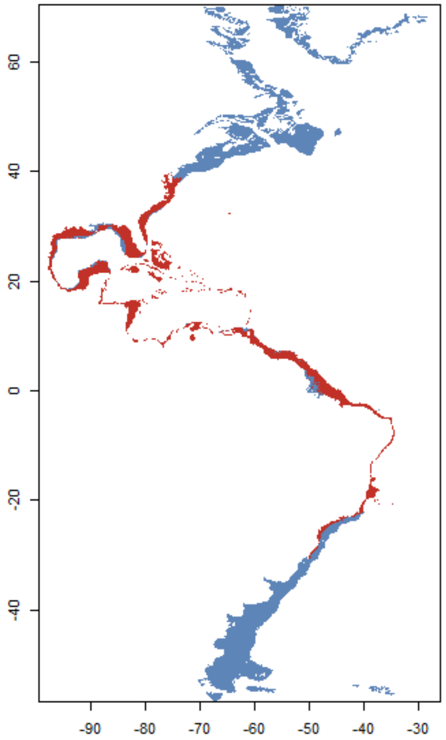
S) **Present**

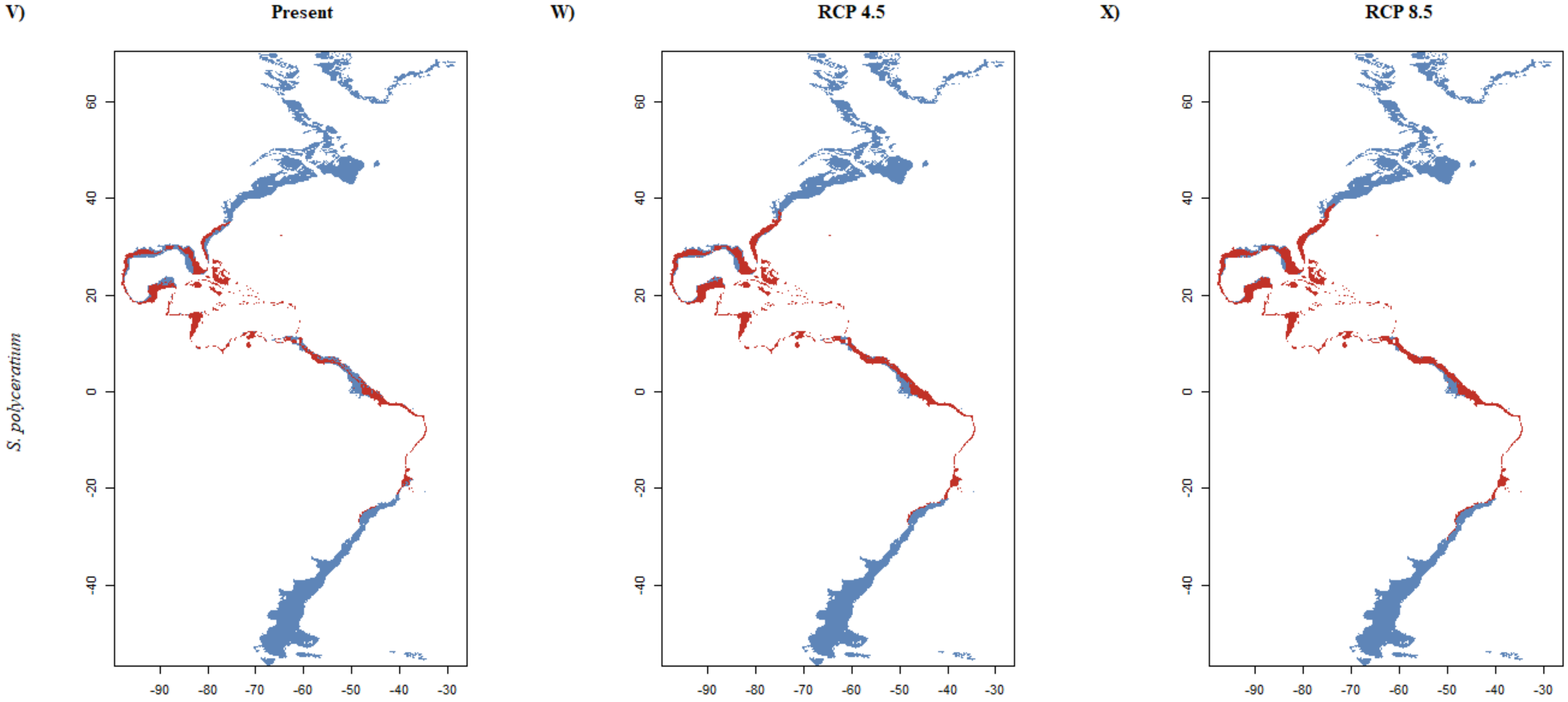


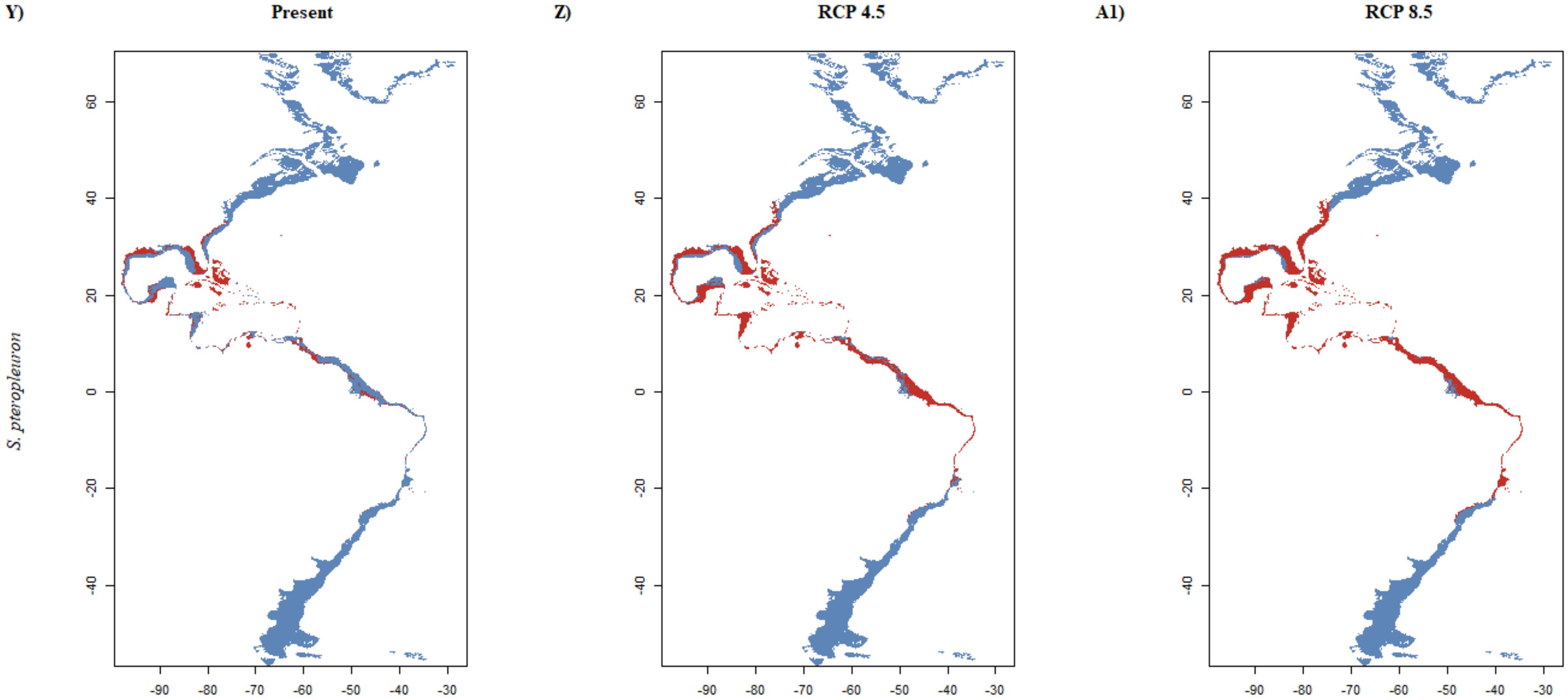
T) **RCP 4.5**

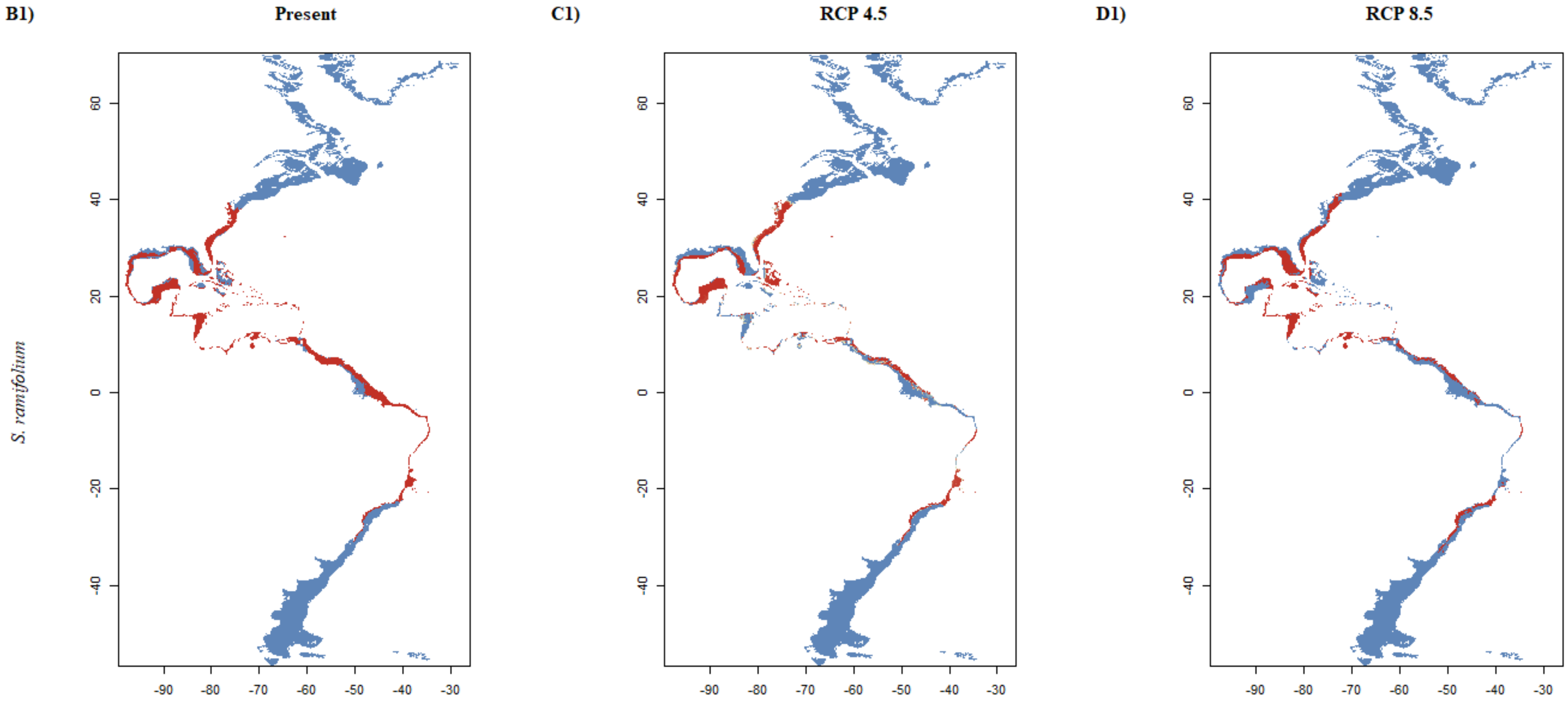


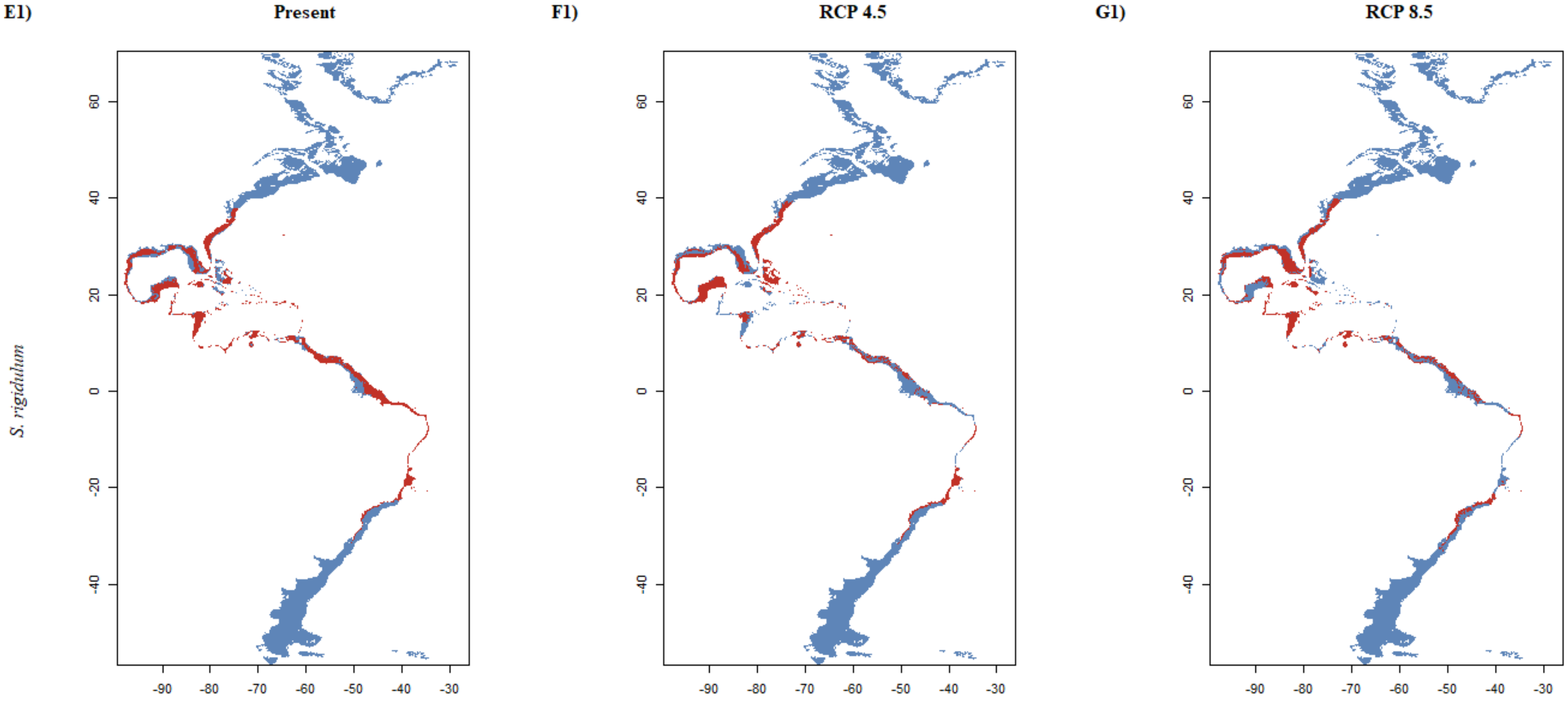
U) **RCP 8.5**




V)
Present
W)
RCP 4.5
X)
RCP 8.5
S. polyceratium
60
40
20
0
-20
-40
-90
-80
-70
-60
-50
-40
-30


Y)
Present
Z)
RCP 4.5
A1)
RCP 8.5
S. pteropleuron
60
40
20
0
-20
-40
-90
-80
-70
-60
-50
-40
-30


B1)
Present
C1)
RCP 4.5
D1)
RCP 8.5
S. ramifolium
60
40
20
0
-20
-40
-90
-80
-70
-60
-50
-40
-30


E1)
Present
F1)
RCP 4.5
G1)
RCP 8.5
S. rigidulum
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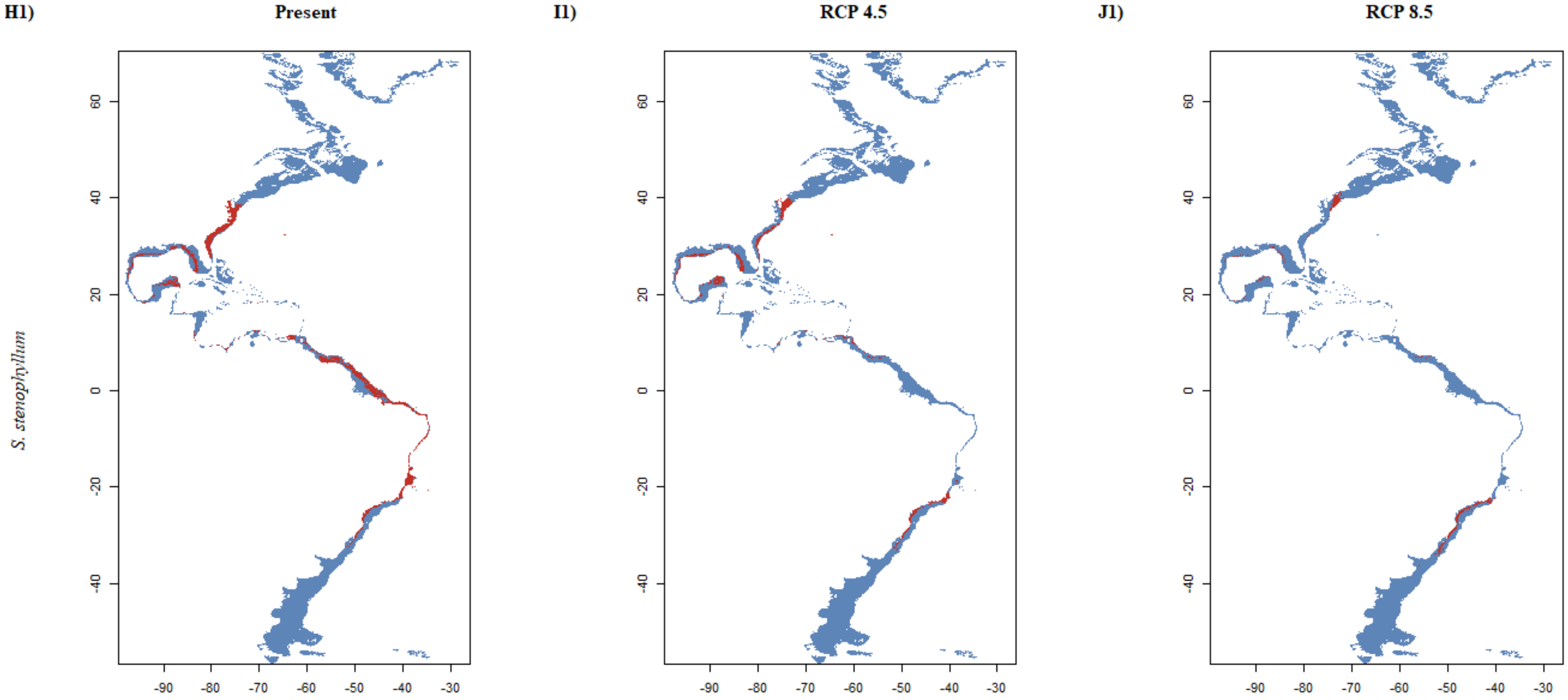
40
20
0
-20
-40
-90
-80
-70
-60
-50
-40
-30


H1)
Present
I1)
RCP 4.5
J1)
RCP 8.5
S. stenophyllum
60
40
20
0
-20
-40
-90
-80
-70
-60
-50
-40
-30

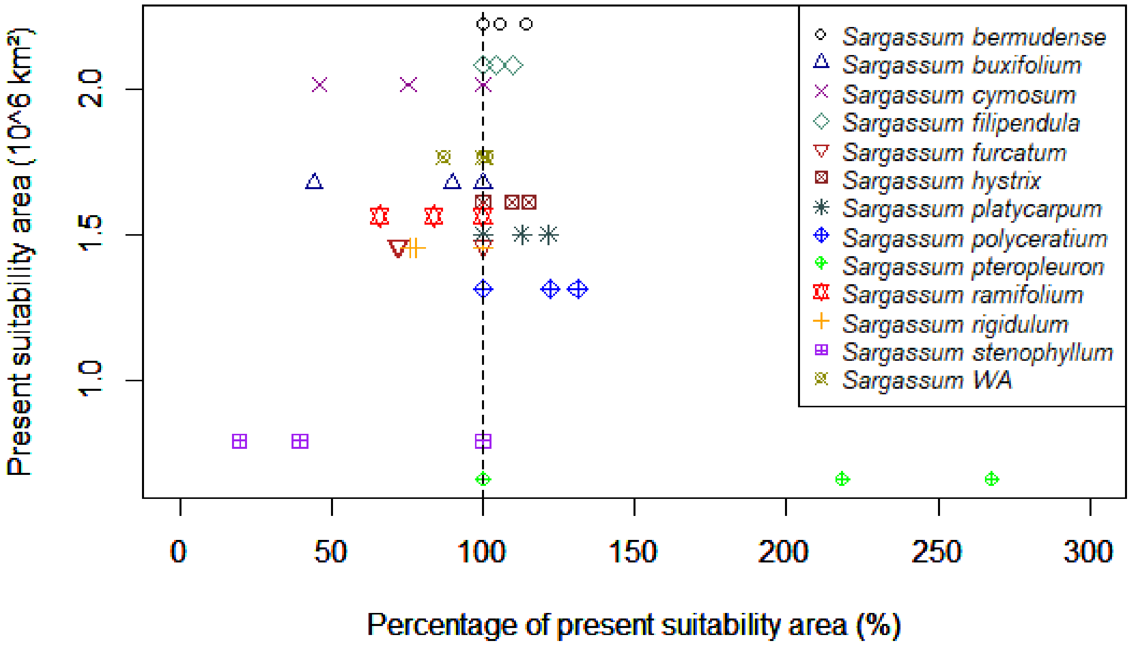


Figure 3. Changes of future suitability area for Western Atlantic *Sargassum* species. Similar dots represent the same species in different projected scenarios. Dashed line represents the projected suitability area for the present scenario. Dots on the left side of the line represent a decrease in suitability area. Dots on the right side highlight an increase in the suitability area. Dots on the dashed line show the present scenario for each species. Dots next to the dashed line show the RCP 4.5 scenario and points further away represent the RCP 8.5 scenario, with exception of *S. furcatum* whose most distant point represents the RCP 4.5 scenario, and *Sargassum* WA whose the dot on the right side of the dashed line represents RCP 4.5 scenario and the dot on the left side represent the RCP 8.5 scenario.

Supplementary Material

Table S1. Values of Area Under Receiver Operating Characteristic Curve (AUC) and true skill statistics (TSS) for each algorithm tested for seven Sargassum species. Models tested: generalized linear model (GLM), generalized additive model (GAM), boosted regression trees (BRT), random forests (RF), Bioclim, classification and regression trees (CART), support vector machine (SVM), artificial neural networks (ANN), maximum likelihood (Maxlike), maximum entropy (Maxent), multivariate adaptive regression spline (MARS).

Figure S1. Phylogenetic relationships of selected *Sargassum* species included in this study, following Camacho *et al.* (2015) and B. Barros-Barreto, M. T. Szechy & V. Cassano (unpublished data).

Figure S2. Variables histogram and their correlation used to fit ecological niche models for *Sargassum* species in the Western Atlantic Ocean.

Figure S3. Correlation between changes in suitability area and changes in latitudinal limits for 13 *Sargassum* species from the Western Atlantic Ocean. A & B: data from the northern hemisphere. C & D: data from the southern hemisphere. A & C: results from RCP 4.5. B & D: results from RCP 8.5. Dashed lines represent regression lines for better pattern visualization. Dots correspond to the same species as in Fig.3. Suitability area corresponds to the future suitability area in relation to the suitability area predicted for the present scenario for each species.

Figure S4. Suitability map for *Sargassum* WA predictions for (A) present, (B) RCP 4.5, and (C) RCP 8.5 scenarios.

Appendix S1 - Considerations of some unchosen model variables

Appendix S2 – Comments on research limitations

Appendix S3 – R scripts used in this study

Table S1. Values of Area Under Receiver Operating Characteristic Curve (AUC) and true skill statistics (TSS) for each algorithm tested for seven *Sargassum* species. Models tested: generalized linear model (GLM), generalized additive model (GAM), boosted regression trees (BRT), random forests (RF), Bioclim, classification and regression trees (CART), support vector machine (SVM), artificial neural networks (ANN), maximum likelihood (MAXLIKE), maximum entropy (MAXENT), and multivariate adaptive regression spline (MARS).

Species/Algorithms	**GLM**		**GAM**		**BRT**		**RF**		**Bioclim**		**CART**		**SVM**		**ANN**		**MAXLIKE**		**MAXENT**		**MARS**	
	AUC	*TSS*	*AUC*	*TSS*	*AUC*	*TSS*	*AUC*	*TSS*	*AUC*	*TSS*	*AUC*	*TSS*	*AUC*	*TSS*	*AUC*	*TSS*	*AUC*	*TSS*	*AUC*	*TSS*	*AUC*	*TSS*
S. cymosum	0.78	0.67	0.82	0.63	0.81	0.67	0.85	0.62	0.84	0.66	0.81	0.63	0.84	0.63	0.81	0.61	0.81	0.62	0.82	0.67	0.81	0.66
S. filipendula	0.83	0.68	0.87	0.72	0.86	0.67	0.91	0.73	0.79	0.60	0.86	0.67	0.89	0.76	0.86	0.66	0.83	0.67	0.86	0.68	0.85	0.66
S. hystrix	0.84	0.67	0.84	0.66	0.81	0.66	0.87	0.68	0.79	0.62	0.84	0.64	0.83	0.68	0.84	0.63	0.82	0.65	0.82	0.67	0.86	0.67
S. platycarpum	0.84	0.73	0.82	0.72	0.89	0.77	0.87	0.77	0.82	0.63	0.84	0.65	0.87	0.75	0.84	0.65	0,84	0.69	0.85	0.77	0.78	0.59
S. polyceratium	0.90	0.77	0.92	0.77	0.90	0.76	0.92	0.80	0.87	0.73	0.90	0.74	0.93	0.80	0.89	0.72	0.85	0.70	0.9o	0.78	0.88	0.77
S. pteropleuron	0.88	0.77	NA	NA	0.87	0.75	0.89	0.76	0.74	0.50	0.81	0.60	0.83	0.68	0.82	0.66	0.77	0.55	0.89	0.77	0.84	0.65
Sargassum WA	0.79	0.57	0.85	0.62	0.85	0.60	0.88	0.63	0.74	0.55	NA	NA	0.86	0.64	0.84	0.58	0.78	0.57	0.84	0.61	0.85	0.63

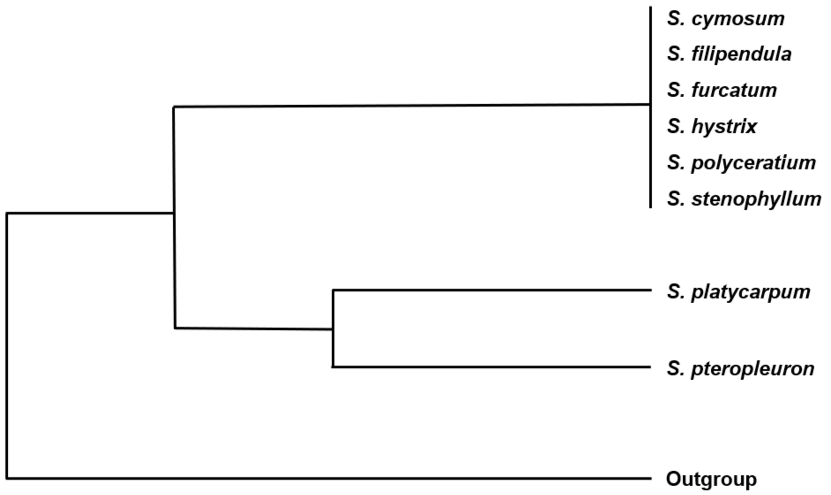


Figure S1. Phylogenetic relationships of selected *Sargassum* species included in this study, following Camacho et al. (2015) and B. Barros-Barreto, M. T. Szechy and V. Cassano (unpublished data)

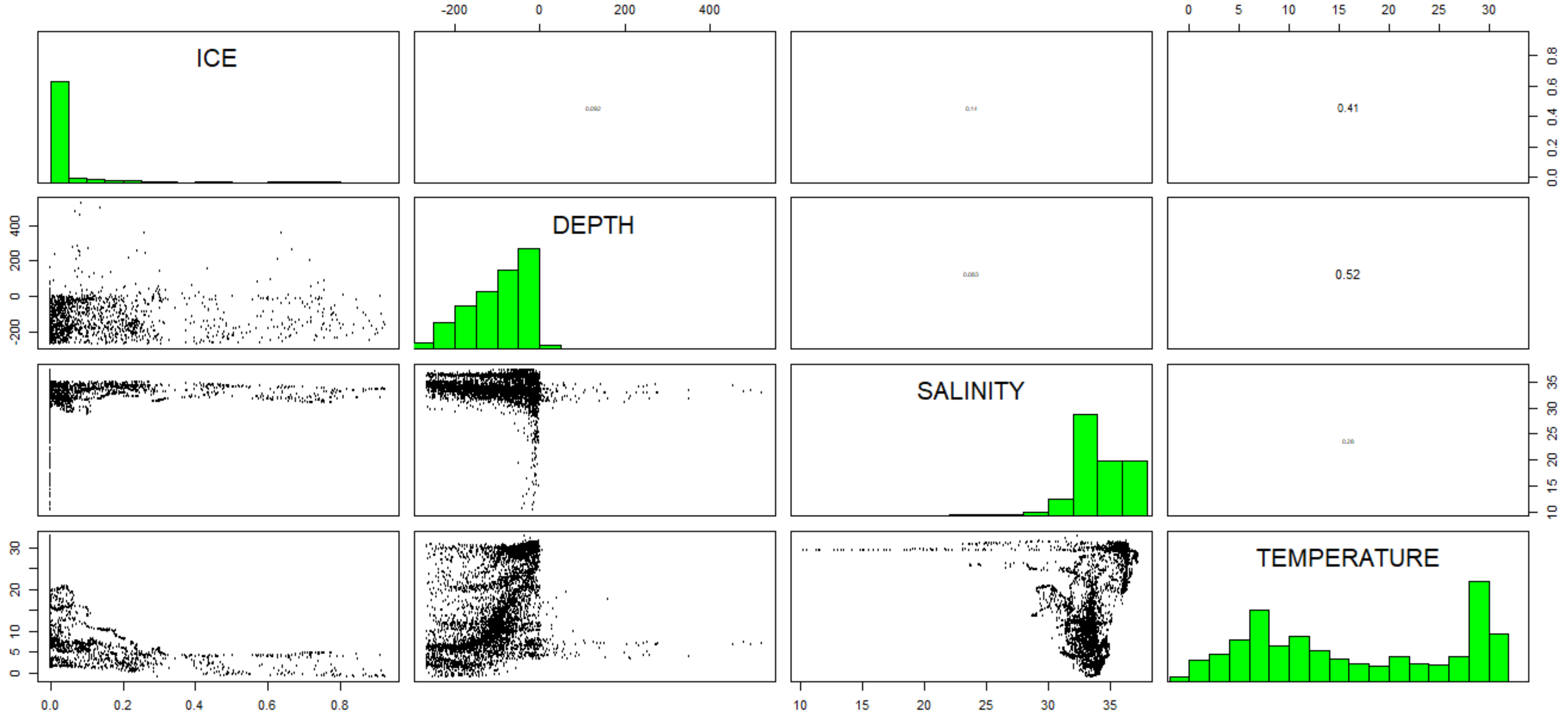


Figure S2. Variables histogram and their correlation used to fit ecological niche models for *Sargassum* species in the Western Atlantic Ocean.

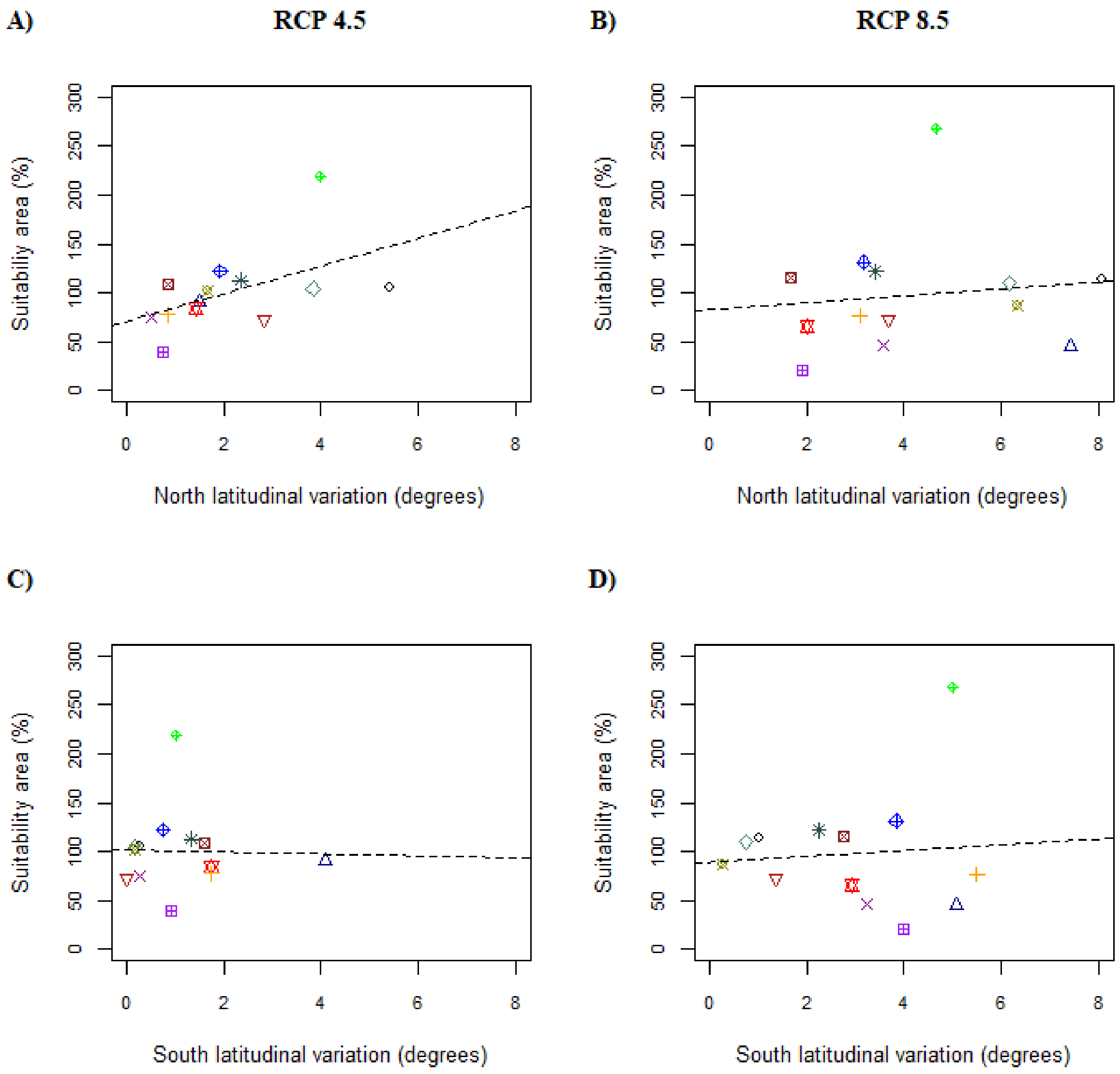


Figure S3. Correlation between changes in suitability area and changes in latitudinal limits for 13 *Sargassum* species from the Western Atlantic Ocean. A & B: data from the northern hemisphere. C & D: data from the southern hemisphere. A & C: results from RCP 4.5. B & D: results from RCP 8.5. Dashed lines represent regression lines for better pattern visualization. Dots correspond to the same species as in Figure 3. Suitability area corresponds to the future suitability area in relation to the suitability area predicted for the present scenario for each species.

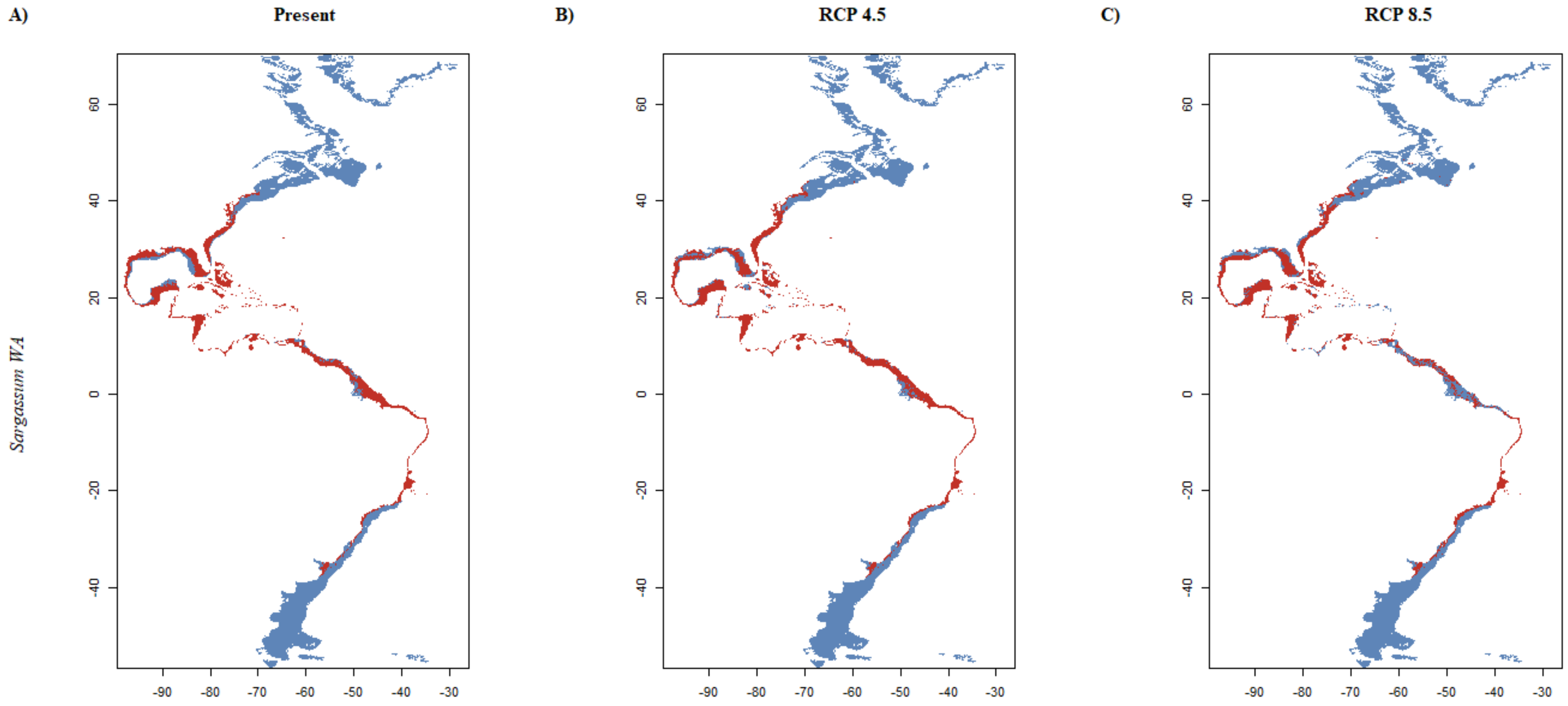


Figure S4. Suitability map for *Sargassum* WA predictions for (A) present, (B) RCP 4.5, and (C) RCP 8.5 scenarios.

Appendix S1 - Considerations of some unchosen model variables

We choose not to use other variables, such as light and nutrient measures. Light is usually correlated with cloud cover and, indirectly, depth. But we aren't able to predict future scenarios for light intensity. We know photon flux density (PFD) requirements for WA benthic *Sargassum* are usually low, and light compensation occurred at reduced intensities when the temperature dropped (Carpenter and Cox 1974, Hanisak and Samuel 1987), possibly not being a limiting parameter in lower depths. However, it must be considered that light is an important factor to consider when we search for deep-water refugia (Graham et al. 2007). Refugia could aid species with lower temperatures requirements to survive in tropical latitudes at higher depths (Wiens 2016). *Sargassum obtusifolium* was found in 200 m depth in Hawaii (De Wreed and Jones 1973, as *S. hawaiensis*).

Also, we cannot predict future scenarios for nitrogen nor phosphorus concentrations in coastal areas, as urban development can rapidly change these nutrients input. Physiological studies with pelagic *Sargassum natans* and *S. fluitans* species found an increase in growth and photosynthetic rate with phosphate enrichment, but not with nitrate or ammonium addiction (Lapointe 1986). Nitrogen and phosphorus concentrations in the North Atlantic Ocean were low to indetectable. However, nitrogen-fixer epiphite *Dichothrix fucicola* usually were found in pelagic *Sargassum* (Carpenter 1972) and *Sargassum* patches interstitial water has 2-3 times more reactive phosphorus concentrations than in surrounding areas (Culliney 1970). Otherwise, recent studies with brown algae have found that neither nitrogen nor phosphorus are important variables in SDM models when one think in the distribution limits of a species. The algae can grow with low nutrient concentrations, but at a slower rate (Franco et al. 2018). Nutrients, however, can increase the upper limit temperature of *Sargassum polycystum* (Zou et al. 2017). Nutrients are also important variables for predicting abundance and biomass, helping to forecast algae blooms (Lapointe 1986, Brooks et al. 2018, Jouanno et al. 2021).

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Appendix S2 – Comments on research limitations

In temperate regions, temperature seasonal variations are more pronounced and directly influence benthic composition. The perennial species in temperate environments – or at least species with perennial holdfast – have been adapted to seasonal physical changes (Hällfors et al. 2016). These variations fit the species' realized niche and must be considered when modeling temperate species. Tropical species, however, evolved in an environment that is climatically more stable, and are hence strongly driven by ecological interactions, microclimate and non-climate driven environmental heterogeneity such as changes in substrate characteristics (Brown 2014).

Nutrients have synergistic effects with CO_2 concentration on seaweed growth, settlement and photosynthesis (Russell et al. 2009). The influence of different nutrient availability and concentration on habitat modeling, such as iron, nitrogen, and phosphorus average concentration have been studied in *Sargassum* and other algae (Miki et al. 2016, Wenke 2019). Iron as a fertilizer eluate, and iron-binding ethylenediaminetetraacetic acid (Fe-EDTA), promote the growth of germlings and immature stages of *Sargassum horneri* in Japan (Miki et al. 2016). Iron depositions are also related to recent accumulation as of drifting pelagic *Sargassum* on Caribbean beaches (Oviatt et al. 2019). Nitrogenase protein contains iron, so iron concentrations act in nitrogen fixation regulation (Wenke 2019). The development of present day and future nutrient rasters could improve *Sargassum* niche distribution models.

Dispersion is an aspect we cannot predict using the ENM approach. Changes in macroalgae suitability area may be faster than dispersion or migration rates towards new suitable habitats, potentially leading to local extinctions (Wiens 2016). Local extinctions due to the inability of a species to move into newly suitable areas has been documented for *Fucus* *vesiculosus* in the Baltic Sea (Jonsson et al. 2018). Local extinctions for other large Fucales have also been observed with *Sargassum* and *Cystoseira* species in the Mediterranean Sea (Thibaut et al. 2005, 2015). WA *Sargassum* usually have air bladders or aerocysts (Paula & Eston 1987, Camacho et al. 2015), and some species like *S. hystrix* and *S. platycarpum* were found floating along the Brazil Current, 100 km offshore (Oliveira-Filho et al. 1979). The effects of the Amazon discharge as a major dispersal barrier are also unknown for *Sargassum* species and it may hinder or even interrupt dispersion from and to the South Atlantic (Floeter et al. 2008). In fact, our present suitability areas suggest the influence of the Amazon River as a barrier to dispersal. *Sargassum* species only known to occur in Northern latitudes (e.g., *S. bermudense* and *S. pteropleuron*) have similar environments in the Southern Hemisphere. Without dispersion, macroalgae survival will depend solely on their capacity to acclimate or to shift their realized niche (Wiens 2016). To work around this issue, physiological experiments can improve the ENM predictions (Ready et al. 2010).

Ecological data like density and abundance may be helpful to foresee some ecosystems services (Gouvêa et al. 2020), and density of predators, epibionts colonization, assemblage resilience, and reproductive seasonality may improve predictions for species and whole communities (Lima 2007, Ling & Johnson 2009, Peck et al. 2018, Kvile et al. 2022).

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Appendix S3 - R scripts used in this study

```
########################################
### Distribution of selected species
# Example with Sargassum cymosum


### Calling packages
if(!require(dismo)){install.packages('dismo'); library(dismo)}
if(!require(rgeos)){install.packages('rgeos'); library(rgeos)}
if(!require(raster)){install.packages('raster'); library(raster)}
if(!require(rgdal)){install.packages('rgdal'); library(rgdal)}
if(!require(leaflet)){install.packages('leaflet'); library(leaflet)}
if(!require(sdmpredictors)){install.packages('sdmpredictors'); library(sdmpredictors)}
if(!require(SDMTools)){install.packages('SDMTools'); library(SDMTools)}
if(!require(sdm)){install.packages('sdm'); library(sdm)}
if(!require(usdm)){install.packages('usdm'); library(usdm)}
if(!require(dplyr)){install.packages('dplyr'); library(dplyr)}
my.colors = colorRampPalette(c("#5E85B8","#EDF0C0","#C13127"))

########################################
##### Environmental variables


### Downloading layers of interest
### Present
prof <- load_layers("BO_bathymin")                            ## depth
temp <- load_layers("BO2_tempmax_bdmin")                 ## temperature
salinidade <- load_layers("BO2_salinitymean_bdmin")      ## salinity
gelo <- load_layers("BO2_icethickmean_ss")                  ## ice


### RCP 4.5 2100
temp.rcp45.2100 <- load_layers("BO2_RCP45_2100_tempmax_bdmin")
sal.rcp45.2100 <- load_layers("BO2_RCP45_2100_salinitymean_bdmin")
gelo.rcp45.2100 <- load_layers("BO2_RCP45_2100_icethickmean_ss")


### RCP 8.5 2100
temp.rcp85.2100 <- load_layers("BO2_RCP85_2100_tempmax_bdmin")
sal.rcp85.2100 <- load_layers("BO2_RCP85_2100_salinitymean_bdmin")
gelo.rcp85.2100 <- load_layers("BO2_RCP85_2100_icethickmean_ss")


### Writing rasters on pc
writeRaster (prof, “prof.tif”)                   ## do the same with the others


### Calling rasters after mask with WA extent provided in QGIS software
### Present
prof <- raster("prof_mask.tif")                      #depth
```

```
temp <- raster("temp_mask.tif")                    #temperature
salinidade <- raster("salinidade_mask.tif")        #salinity
gelo <- raster("gelo_mask.tif")                    #ice

#### RCP 4.5 2100
temp.rcp45.2100 <- raster("temp.rcp45.2100_mask.tif")
sal.rcp45.2100 <- raster("sal.rcp45.2100_mask.tif")
gelo.rcp45.2100 <- raster("gelo.rcp45.2100_mask.tif")

#### RCP 8.5 2100
temp.rcp85.2100 <- raster("temp.rcp85.2100_mask.tif")
sal.rcp85.2100 <- raster("sal.rcp85.2100_mask.tif")
gelo.rcp85.2100 <- raster("gelo.rcp85.2100_mask.tif")

### Creating extent of 26m depth
WA = prof
WA [ WA>=(-265)] =1
WA [ WA<(-265)]= NA
plot (WA, col="blue", legend=F)

##############################################
##### Present

### Creating stack with environmental layers
varbio.stack.presente <- stack (gelo, prof, salinidade, temp)
### Masking environmental layers with depth 265m layer
varbio.m <- mask (varbio.stack.presente, WA)
### Excluding NA's cells (depth > 265m)
varbio.m <- trim (varbio.m)

writeRaster (varbio.m, "varbio.m_270m.tif")
##############################################
##### RCP 4.5 em 2100

varbio.stack.rcp45.2100 <- stack (gelo.rcp45.2100, prof, sal.rcp45.2100,
temp.rcp45.2100)
varbio.m.rcp45.2100  <- mask (varbio.stack.rcp45.2100 , WA)
varbio.m.rcp45.2100 <- trim (varbio.m.rcp45.2100)
names(varbio.m.rcp45.2100) =c("gelo", "profundidade", "salinidade", "temperatura")

##############################################
##### RCP 8.5 em 2100

varbio.stack.rcp85.2100 <- stack (gelo.rcp85.2100, prof, sal.rcp85.2100,
temp.rcp85.2100)
```

```
varbio.m.rcp85.2100  <- mask (varbio.stack.rcp85.2100 , WA)
varbio.m.rcp85.2100 <- trim (varbio.m.rcp85.2100)
names(varbio.m.rcp85.2100) = c("gelo", "profundidade", "salinidade", "temperatura")

########################################
##### Colinearity

### Checking correlation between variables
varbio.val <- getValues(varbio.m)            ## extracting values
varbio.coord <- coordinates (varbio.m)       ## extraindo coordinate
varbio.j <- cbind (varbio.coord, varbio.val)
varbio.df <- na.omit (varbio.j)
write.table(varbio.df.presente, "bioclimatica.csv")

var.cor <- cor (varbio.df)
var.cor

### Potting (Figure S2)
names (varbio.m) = c ("ice", "depth", "salinity", "temperature")

panel.hist <- function(x, ...)
{
  usr <- par("usr"); on.exit(par(usr))
  par(usr = c(usr[1:2], 0, 1.5) )
  h <- hist(x, plot = FALSE)
  breaks <- h$breaks;
  nB <- length(breaks)
  y <- h$counts; y <- y/max(y)
  rect(breaks[-nB], 0, breaks[-1], y, col="cyan", ...)
}

panel.cor <- function(x, y, digits=2, prefix="", cex.cor, ...)
{
  usr <- par("usr"); on.exit(par(usr))
  par(usr = c(0, 1, 0, 1))
  r <- abs(cor(x, y))
  txt <- format(c(r, 0.2), digits=digits)[1]
  txt <- paste(prefix, txt, sep="")
  if(missing(cex.cor)) cex.cor <- 0.8/strwidth(txt)
  text(0.5, 0.5, txt, cex = 1)
}

### Figure S2
pairs(varbio.m, panel=panel.smooth, diag.panel=panel.hist, lower.panel=panel.cor)
```

```
### Other way to test colinearity
v1 <- usdm::vifstep(varbio.stack.presente)
v1
v1@results     ### Ideal = all VIFs < 4
######################################
###### Occurrence data


### Calling table (without duplicate registers)
o <- read.table ("Scymosum_limpo_preview.csv", head=T, dec=".", sep=",")
lat.lon01 <- cbind (o$lon, o$lat)                ## latitude and longitude coordinates
pts01 <-SpatialPoints(lat.lon01)


### Excluding registers out of 265m depth
clim.pts01 <- cbind (lat.lon01, extract (varbio.m, pts01, cellnumbers=T) )
clim2.pts01 <- na.omit(clim.pts01)
write.table (clim2.pts01, "scymosum_limpo.txt")
######################################
###### Pseudo-Absence / Background data


### Extracting values
varbio.model <- varbio.df  #[, c("x", "y", "gelo", "prof", "sal", "temp")]


### Making a subset of the total number of registers to be used
backtotal <- varbio.model [sample(1:nrow(varbio.model),
                          nrow(clim2.pts01)),]
clim3.pts01 <- SpatialPoints(clim2.pts01)


### Checking if the points generate makes biological features
plot (varbio.m[[2]], legend=F, main="Presença e background")
points (backtotal[,1:2], add=T, col="firebrick", cex=0.5, pch=16)
points (clim3.pts01, add=T, pch=16, cex=0.5, col="blue")


write.table(backtotal, "background.txt")


### Saving background and presence in the same object
### Add 1 for presence and 0 for pseudo-absence
pts.presente <- clim2.pts01[,1:2]              # presence
pts.presente <- as.data.frame(pts.presente)
colnames(pts.presente) <- c("x", "y")
pts.presente$pb <- rep(1, nrow(pts.presente))


backtotal.presente <- backtotal[,1:2]                  # pseudo-absence
backtotal.presente <- as.data.frame(backtotal.presente)
backtotal.presente$pb <- rep(0,nrow(pts.presente))
str(backtotal.presente)
```

```
data.presente <- rbind(pts.presente, backtotal.presente)
r2 <- SpatialPointsDataFrame(data.presente[,1:2], data.presente)


write.table (data.presente, "pb.txt")
########################################
##### Creating the model for current/present scenario


### Preparing objects
preds = varbio.m
dados1 = clim2.pts01
names(preds) <- c("gelo", "profundidade", "salinidade", "temperatura")
profundidade = prof
temperatura = temp


### ENM
d <- sdm::sdmData(formula=pb ~ gelo + profundidade +salinidade + temperatura,
        train=r2,
        predictors=preds)
d


model1<-sdm(pb ~ gelo + profundidade +salinidade + temperatura,
        data=d,
        #methods=c('glm', 'gam', "brt", "rf", "bioclim","cart", "fda", nnetMLP
        #"svm","rpart", "mda", "maxlike", "maxent", "mars", "glmnet","bioclimD" ),
        methods=c('glm', 'gam', "brt", "rf", "bioclimD", "cart",
                "svm","rpart", "maxlike", "maxent", "mars"),
        replications='sub', test.percent=25, n=10)
model1
roc(model1, smooth=T)
write.sdm(model1,"model.presente_Scymosum.sdm")


### Viewing model informations
getModelInfo(model1)
v1<- getVarImp(model1, id=1, wtest='test.dep')            ## variables importance
v1
plot(v1)


### Predicting
p2.presente <- predict(model1,newdata=preds, type='response',
                overwrite=T)
outfile2 <- writeRaster(p2.presente, filename='pred.presente.scymosum.tif',
                          format="GTiff", overwrite=TRUE,
                options=c("INTERLEAVE=BAND","COMPRESS=LZW"))
str(p2.presente)
```

```
### Accessing AUC and TSS
AUCS_model1<-getEvaluation(model1,stat='AUC',wtest='test.dep', opt=1)
AUCS_model1
TSS_model1 <- getEvaluation(model1,stat='tss',wtest='test.dep', opt=1)
TSS_model1


### Checking specific algorithm parameter
p1<- p2.presente
sd.glm<-calc(p1[[1:10]], fun=sd)
sd.glm<-scale(sd.glm)
plot(sd.glm,col=my.colors(1000),main="GLM - VARIAÇÃO")


### Ensemble forecasting using AUC as parameter (example)
w<-AUCS_model2[1:10,2]
w<-w/sum(w)
ens.glm<- p1[[1]]*w[1]+p1[[2]]*w[2]+p1[[3]]*w[3]+p1[[4]]*w[4]+p1[[5]]*w[5]+
  p1[[6]]*w[6]+p1[[7]]*w[7]+p1[[8]]*w[8]+p1[[9]]*w[9]+p1[[10]]*w[10]
plot(ens.glm,col=my.colors(1000), main = "ENSEMBLE - GLM")


### Emsemble Forecasting with all model predictions
            ensemble.tss <- sdm::ensemble (model1, newdata=preds,
                              filename='ensemble.full.tss.cymosum.img',
                              setting=list(method='weighted',stat='tss'),
                              overwrite=T)
writeRaster(ensemble.tss,"ensemble.presente_Scymosum.tif")


plot (ensemble.tss, col=my.colors(1000))
points(clim2.pts01, col="dark green", pch=16, cex=0.5)


### Binarizing
ensemble.tss.presente <- ensemble.tss
ensemble.tss.presente[ensemble.tss.presente>=0.5]=1
ensemble.tss.presente[ensemble.tss.presente<0.5]=0
plot (ensemble.tss.presente,  col=my.colors(1000))
points(clim2.pts01, col="dark green", pch=16, cex=0.5)


writeRaster (ensemble.tss.presente, "ensemble.tss.presente_Scymosum.tif")


### Accessing coordinates of binarized ensemble
ensemble.bin.1 <- ensemble.tss.presente
ensemble.bin.1 [ensemble.bin.1>=1]=1
ensemble.bin.1 [ensemble.bin.1<0.5]=NA
ensemble.bin.1 <- trim(ensemble.bin.1)
ensemble.bin.1
table (getValues(ensemble.bin.1))              # number of cells occupied
```

```
### Area
cell_size1<-area(ensemble.bin.1, na.rm=TRUE, weights=F)
cell_size1<-cell_size1[!is.na(cell_size1)]
raster_area.presente<-  sum (cell_size1[1:length(cell_size1)])
raster_area.presente


### Intersection with present occurrence (overlap)
overlap.pres <- intersect(ensemble.bin.1, ensemble.tss.presente)
x <- brick(resample(ensemble.bin.1, overlap.pres, method = "ngb"),
        resample(ensemble.tss.presente, overlap.pres, method = "ngb"))

plot(ensemble.tss.presente, col = "blue")
image(ensemble.bin.1, add = TRUE, col = "green")
image(x, add = TRUE, col = "red")


sum(values(area(ensemble.bin.1)))          ## suitability area


########################################
##### Prediction for RCP 4.5 2010 scenario


p.rcp.45.2100 <- predict(model1,newdata=varbio.m.rcp45.2100, type='response',
                 overwrite=T)
outfile3 <- writeRaster(p.rcp.45.2100, filename='p.rcp.45.2100_Scymosum.tif',
                                   format="GTiff",                    overwrite=TRUE,
                         options=c("INTERLEAVE=BAND","COMPRESS=LZW"))
str(p.rcp.45.2100)


ensemble.tss.rcp45 <- sdm::ensemble (model1, newdata=varbio.m.rcp45.2100,
                         filename='ensemble.full.tss.rcp45.Scymosum.img',
                        setting=list(method='weighted',stat='tss'),
                        overwrite=T)
writeRaster(ensemble.tss.rcp45,"ensemble.rcp45_Scymosum.tif")


### Binarize ensemble
ensemble.tss.rcp.45.bin <- ensemble.tss.rcp45
ensemble.tss.rcp.45.bin[ensemble.tss.rcp.45.bin>=0.5]=1
ensemble.tss.rcp.45.bin[ensemble.tss.rcp.45.bin<0.5]=0


writeRaster (ensemble.tss.rcp.45.bin, "ensemble.tss.bin.rcp45_Scymosum.tif")


### Accessing coordinates of binarized ensemble
ensemble.bin.2 <- ensemble.tss.rcp.45.bin
ensemble.bin.2 [ensemble.bin.2>=1]=1
ensemble.bin.2 [ensemble.bin.2<0.5]=NA
```

```
ensemble.bin.2 <- trim(ensemble.bin.2)
ensemble.bin.2
table (getValues(ensemble.bin.2))


### Intersection with present occurrence (overlap)
overlap.pres <- intersect(ensemble.bin.2, ensemble.bin.1)
x2 <- brick(resample(ensemble.bin.2, overlap.pres, method = "ngb"),
         resample(ensemble.bin.1, overlap.pres, method = "ngb"))
table (getValues(ensemble.bin.2))
table (getValues(overlap.pres))


plot(ensemble.tss.presente, col = "blue", legend=F)
image(ensemble.bin.2, add = TRUE, col = "red")
image(overlap.pres, add = TRUE, col = "green")


### Area - get sizes of all cells in raster [km2]
cell_size.rcp45<-area(ensemble.bin.2, na.rm=TRUE, weights=F)
### delete NAs from vector of all raster cells
cell_size.rcp45<-cell_size.rcp45[!is.na(cell_size.rcp45)]
### compute area [km2] of all cells in geo_raster
raster_area.rcp.45<- sum (cell_size.rcp45[1:length(cell_size.rcp45)])
raster_area.rcp.45


### Overlapping Area
cell_size3<-area(overlap.pres, na.rm=TRUE, weights=F)
cell_size3<-cell_size3[!is.na(cell_size3)]
raster_area.overlap.rcp45 <- sum (cell_size3[1:length(cell_size3)])
raster_area.overlap.rcp45

### Overlapping percentage
overlap.total.rcp45 = raster_area.overlap.rcp45 / raster_area.presente
overlap.total.rcp45
########################################
##### Prediction for RCP 8.5 2010 scenario


p.rcp.85.2100 <- predict(model1,newdata=varbio.m.rcp85.2100, type='response',
                  overwrite=T)
outfile3 <- writeRaster(p.rcp.85.2100, filename='p.rcp.85.2100_Scymosum.tif',
                              format="GTiff",                 overwrite=TRUE,
                         options=c("INTERLEAVE=BAND","COMPRESS=LZW"))
str(p.rcp.85.2100)


ensemble.tss.rcp85 <- sdm::ensemble(model1,newdata=varbio.m.rcp85.2100,
                       filename='ensemble.full.tss.rcp85.Scymosum.img',
                       setting=list(method='weighted',stat='tss'),
                       overwrite=T)
```

```
writeRaster(ensemble.tss.rcp85,"ensemble.rcp85_Scymosum.tif")

### Binarize ensemble
ensemble.tss.rcp.85.bin <- ensemble.tss.rcp85
ensemble.tss.rcp.85.bin[ensemble.tss.rcp.85.bin>=0.5]=1
ensemble.tss.rcp.85.bin[ensemble.tss.rcp.85.bin<0.5]=0
plot (ensemble.tss.rcp.85.bin, legend=F, col=my.colors(1000))
#ensemble.bin.tss.rcp85_Scymosum.png

writeRaster (ensemble.tss.rcp.85.bin, "ensemble.tss.bin.rcp85_Scymosum.tif")

### Accessing coordinates of binarized ensemble
ensemble.bin.3 <- ensemble.tss.rcp.85.bin
ensemble.bin.3 [ensemble.bin.3>=1]=1
ensemble.bin.3 [ensemble.bin.3<0.5]=NA
ensemble.bin.3 <- trim(ensemble.bin.3)
ensemble.bin.3
table (getValues(ensemble.bin.3))

### Intersection with present occurrence (overlap)
overlap.rcp85 <- intersect(ensemble.bin.3, ensemble.bin.1)
x2 <- brick(resample(ensemble.bin.3, overlap.rcp85, method = "ngb"),
         resample(ensemble.bin.1, overlap.rcp85, method = "ngb"))
table (getValues(ensemble.bin.3))
table (getValues(overlap.rcp85))

plot(ensemble.tss.presente, col = "blue", legend=F)
image(ensemble.bin.3, add = TRUE, col = "red")
image (overlap.rcp85, col="green", add=T)

### Area - get sizes of all cells in raster [km2]
cell_size.rcp85<-area(ensemble.bin.3, na.rm=TRUE, weights=F)
cell_size.rcp85<-cell_size.rcp85[!is.na(cell_size.rcp85)]
raster_area.rcp.85 <- sum (cell_size.rcp85[1:length(cell_size.rcp85)])
raster_area.rcp.85

### Overlapping area
cell_size.085 <- area(overlap.rcp85, na.rm=TRUE, weights=F)
cell_size.085 <- cell_size.085[!is.na(cell_size.085)]
            raster_area.overlap.rcp85 <- sum (cell_size.085 [1:length(cell_size.085)])
raster_area.overlap.rcp85

### Overlapping percentage
overlap.total.rcp85 = raster_area.overlap.rcp85 / raster_area.presente
overlap.total.rcp85
```

```
####################################
####################################
##### Creating ensemble of species modelled with LOOCV approach
### Example with Sargassum bermudense


### Reading object with Fixed cumulative value 10 Cloglog threshold values
t10 <- read.table ("t10.csv", sep=";", head=T)
t10 <- t10[,2]


### Calling rasters created with Maxent.jar
### Numbers of rasters equal number of observations/presence
{r01.bin <- raster("Sargassum_bermudense_0_layers presente 4v.asc")
 r01.bin[r01.bin <= t10[1]] = 0
 r01.bin[r01.bin > t10[1]] = 1}
{r02.bin <- raster("Sargassum_bermudense_1_layers presente 4v.asc")
 r02.bin[r01.bin <= t10[2]] = 0
 r02.bin[r01.bin > t10[2]] = 1}
{r03.bin <- raster("Sargassum_bermudense_2_layers presente 4v.asc")
  r03.bin[r03.bin <= t10[3]] = 0
  r03.bin[r03.bin > t10[3]] = 1}
{r04.bin <- raster("Sargassum_bermudense_3_layers presente 4v.asc")
  r04.bin[r04.bin <= t10[4]] = 0
  r04.bin[r04.bin > t10[4]] = 1}
{r05.bin <- raster("Sargassum_bermudense_4_layers presente 4v.asc")
  r05.bin[r05.bin <= t10[5]] = 0
  r05.bin[r05.bin > t10[5]] = 1}
{r06.bin <- raster("Sargassum_bermudense_5_layers presente 4v.asc")
  r06.bin[r06.bin <= t10[6]] = 0
  r06.bin[r06.bin > t10[6]] = 1}
{r07.bin <- raster("Sargassum_bermudense_6_layers presente 4v.asc")
  r07.bin[r07.bin <= t10[7]] = 0
  r07.bin[r07.bin > t10[7]] = 1}
{r08.bin <- raster("Sargassum_bermudense_7_layers presente 4v.asc")
  r08.bin[r08.bin <= t10[8]] = 0
  r08.bin[r08.bin > t10[8]] = 1}
{r09.bin <- raster("Sargassum_bermudense_8_layers presente 4v.asc")
  r09.bin[r09.bin <= t10[9]] = 0
  r09.bin[r09.bin > t10[9]] = 1}
{r10.bin <- raster("Sargassum_bermudense_9_layers presente 4v.asc")
  r10.bin[r10.bin <= t10[10]] = 0
  r10.bin[r10.bin > t10[10]] = 1}
{r11.bin <- raster("Sargassum_bermudense_10_layers presente 4v.asc")
  r11.bin[r11.bin <= t10[11]] = 0
  r11.bin[r11.bin > t10[11]] = 1}


### Ensemble
ensemble.p4v <- sum (r01.bin, r02.bin, r03.bin, r04.bin, r05.bin,
                     r06.bin, r07.bin, r08.bin, r09.bin, r10.bin, r11.bin)
```

```
### Binarize ensemble
ensemble.p4v [ensemble.p4v < nrow(points)/2] = 0
ensemble.p4v [ensemble.p4v >= nrow(points)/2] = 1

writeRaster (ensemble.p4v, "ensemble.bin.t10.presente_Sbermudense_maxent_default.tif")


####################################
####################################
##### Analysis

### Read results table
results <- read.table ("Resultados.csv", head=T, dec=".", sep=",")
colnames(results) = c("Species", "Scenario", "Area", "Perc.Area", "S", "dS", "N", "dN", "Overlap Area", "Perc.Overlap")
results <- arrange (results, Species)
attach(results)
spp = (Species[Scenario == "present"])

##### Figure 3 - Changes in future suitability area
windows()
legcolors = c("black", "darkblue", "darkmagenta", "aquamarine4", "firebrick", "brown4", "darkslategrey", "blue", "green", "red", "orange",  "purple", "yellow4")
plot ((Area[Scenario == "present"]/10^6) ~ Perc.Area[Scenario == "present"],
        ylab = "Present suitability area (10^6 km²)",
        xlab= "Percentage of present suitability area (%)",
        pch=c(1:2,4:11, 3, 12:13),
        col=legcolors,
        xlim=c(0,300))
par(new=TRUE)
plot ((Area[Scenario == "present"]/10^6) ~ Perc.Area[Scenario == "RCP 4.5"],
        pch=c(1:2,4:11, 3, 12:13),
        col=legcolors,
        xlim=c(0,300))
par(new=TRUE)
plot ((Area[Scenario == "present"])/10^6 ~ Perc.Area[Scenario == "RCP 8.5"],
        pch=c(1:2,4:11, 3, 12:13),
        col=legcolors,
        xlim=c(0,300))
abline(v = c(100), col="black", lwd=1, lty=2)
legend ("topright", legend=spp,
        col=legcolors,
        pch=c(1:2,4:11, 3, 12:13),
        cex=0.8, text.font=3)
```

```
##### Figure 1. Relation between maximum latitude with suitability area in the
# present scenario for each Western Atlantic Sargassum species and the latitudinal
# variation predicted in our model results


windows()
par(mfrow=c(1,2))


### North
plot (N[Scenario == "present"] ~ dN [Scenario == "present"], #main="present",
        col=legcolors,
        pch=c(1:2,4:11, 3, 12:13),
        xlim=c(0,10),
        xlab="North latitudinal variation (degrees)",
        ylab="Maximum present North latitude (degrees)")
par(new=TRUE)
plot (N[Scenario == "present"] ~ dN [Scenario == "RCP 4.5"], #main="RCP 4.5",
        col=legcolors,
        pch=c(1:2,4:11, 3, 12:13),
        xlim=c(0,10),
        xlab="North latitudinal variation (degrees)",
        ylab="Maximum present North latitude (degrees)")
par(new=TRUE)
plot (N[Scenario == "present"] ~ dN [Scenario == "RCP 8.5"], #main="RCP 8.5",
        col=legcolors,
        pch=c(1:2,4:11, 3, 12:13),
        xlim=c(0,10), xlab="", ylab="")
legend ("bottomright", legend=spp,
        col=legcolors,
        pch=c(1:2,4:11, 3, 12:13),
        cex=0.5, text.font=3)
mtext("A)", side=3, line=2, at=-2.5, cex=1, family="serif")


### South
#S[Scenario == "present"] = S[Scenario == "present"]*(-1)
plot ((S[Scenario == "present"]) ~ dS [Scenario == "present"],
        ylab="Maximum present South Latitude (degrees)",
        xlab="South latitudinal variation (degrees)",
        col=legcolors,
        pch=c(1:2,4:11, 3, 12:13),
        xlim=c(0, 10))
par(new=TRUE)
plot ((S[Scenario == "present"]) ~ dS[Scenario == "RCP 4.5"],
        ylab="Maximum present South Latitude (degrees)",
        xlab="South latitudinal variation (degrees)",
        col=legcolors,
        pch=c(1:2,4:11, 3, 12:13),
        xlim=c(0, 10))
par(new=TRUE)
```

```
plot ((S[Scenario == "present"]) ~ dS [Scenario == "RCP 8.5"],
        xlab="", ylab="",
        col=legcolors,
        pch=c(1:2,4:11, 3, 12:13),
        xlim=c(0, 10))
legend ("bottomright", legend=spp,
        col=legcolors,
        pch=c(1:2,4:11, 3, 12:13),
        cex=0.5, text.font=3)
mtext("B)", side=3, line=2, at=-2.5, cex=1, family="serif")

### Figure S3. Correlation between changes in suitability area and changes in
# latitudinal limits for 13 Sargassum species from the Western Atlantic Ocean.

par(mfrow=c(2,2))
plot (Perc.Area[Scenario == "RCP 4.5"] ~ dN[Scenario == "RCP 4.5"],
        col=legcolors,
        xlim=c(0,8),
        ylim=c(0,300),
        cex.axis =0.8,
        ylab="Suitabiliy area (%)",
        xlab = "North latitudinal variation (degrees)",
        pch=c(1:2,4:11, 3, 12:13))
abline (lm (Perc.Area[Scenario == "RCP 4.5"] ~ dN[Scenario == "RCP 4.5"]), lty=2)
mtext("A)", side=3, line=2, at=-2.2, cex=1, family="serif", font=2)
mtext("RCP 4.5", side=3, line=2, at=4, cex=1, family="serif", font=2)

plot (Perc.Area[Scenario == "RCP 8.5"] ~ dN[Scenario == "RCP 8.5"],
        col=legcolors,
        xlim=c(0,8),
        ylim=c(0,300),
        ylab="Suitabiliy area (%)",
        xlab = "North latitudinal variation (degrees)",
        cex.axis =0.8,
        pch=c(1:2,4:11, 3, 12:13))
abline (lm (Perc.Area[Scenario == "RCP 8.5"] ~ dN[Scenario == "RCP 8.5"]), lty=2)
mtext("B)", side=3, line=2, at=-2.2, cex=1, family="serif", font=2)
mtext("RCP 8.5", side=3, line=2, at=4, cex=1, family="serif", font=2)

plot (Perc.Area[Scenario == "RCP 4.5"] ~ dS[Scenario == "RCP 4.5"],
        col=legcolors,
        xlim=c(0,8),
        ylim=c(0,300),
        ylab="Suitability area (%)",
        xlab = "South latitudinal variation (degrees)",
        cex.axis =0.8,
        pch=c(1:2,4:11, 3, 12:13))
```

```
abline (lm (Perc.Area[Scenario == "RCP 4.5"] ~ dS[Scenario == "RCP 4.5"]), lty=2)
mtext("C)", side=3, line=2, at=-2.2, cex=1, family="serif", font=2)


plot (Perc.Area[Scenario == "RCP 8.5"] ~ dS[Scenario == "RCP 8.5"],
        col=legcolors,
        xlim=c(0,8),
        ylim=c(0,300),
        cex.axis =0.8,
        ylab="Suitability area (%)",
        xlab = "South latitudinal variation (degrees)",
        pch=c(1:2,4:11, 3, 12:13))
abline (lm (Perc.Area[Scenario == "RCP 8.5"] ~ dS[Scenario == "RCP 8.5"]), lty=2)
mtext("D)", side=3, line=2, at=-2.2, cex=1, family="serif", font=2)


##### Spearman correlation tests
### Correlation between latitudinal variation and change in percentual suitability area
cor.test (dS[Scenario == "RCP 4.5"], Perc.Area[Scenario == "RCP 4.5"],
        method ="spearman", alt="greater")          # non significant
cor.test (dS[Scenario == "RCP 8.5"], Perc.Area[Scenario == "RCP 8.5"],
        method ="spearman", alt="greater")          # non significant
cor.test (dN[Scenario == "RCP 4.5"], Perc.Area[Scenario == "RCP 4.5"],
        method ="spearman", alt="greater")                  # significant
cor.test (dN[Scenario == "RCP 8.5"], Perc.Area[Scenario == "RCP 8.5"],
        method ="spearman", alt="greater")          # non significant


### Correlation between overlap areas and changes in percentual suitability area
cor.test (Perc.Area[Scenario == "RCP 4.5"], Perc.Overlap[Scenario == "RCP 4.5"],
        method ="spearman", alt="greater")                  # significant
cor.test (Perc.Area[Scenario == "RCP 8.5"], Perc.Overlap[Scenario == "RCP 8.5"],
        method ="spearman", alt="greater")                  # significant



#########################################
#########################################
##### Variables Importance
###  Example with Sargassum WA


model.SWA = read.sdm("model.presente_SSargassumWA.sdm")
teste = function (i) {
  var.imp <- sdm::getVarImp(model.SWA, id=i)
  var.imp
  imp <- var.imp@varImportance
  ice = imp$corTest[imp$variables== "gelo"]
  temperature = imp$corTest[imp$variables== "temperatura"]
  depth = imp$corTest[imp$variables== "profundidade"]
  salinity= imp$corTest[imp$variables== "salinidade"]
  imp <- cbind (ice, depth, salinity, temperature)
```

```
 colnames (imp) = c("ice", "depth", "salinity", "temperature")
 return (imp)
}
f <- function (i) {
 s<- rbind(
        # GLM
        #teste (i+1),teste (i+2),teste (i+3),teste (i+4),teste (i+5),
        #teste (i+6),teste (i+7),teste (i+8),teste (i+9),teste (i+10),
        # GAM
        teste (i+11),teste (i+12),teste (i+13),teste (i+14),teste (i+15),
        teste (i+16),teste (i+17),teste (i+18),teste (i+19),teste (i+20),
        # BRT
        teste (i+21),teste (i+22),teste (i+23),teste (i+24),teste (i+25),
        teste (i+26),teste (i+27),teste (i+28),teste (i+29),teste (i+10),
        # RF
        teste (i+31),teste (i+32),teste (i+33),teste (i+34),teste (i+35),
        teste (i+36),teste (i+37),teste (i+38),teste (i+39),teste (i+40),
        # BC
        #teste (i+41),teste (i+42),teste (i+43),teste (i+44),teste (i+45),
        #teste (i+46),teste (i+47),teste (i+48),teste (i+49),teste (i+50),
        # CART
        teste (i+51),teste (i+52),teste (i+53),teste (i+54),teste (i+55),
        teste (i+56),teste (i+57),teste (i+58),teste (i+59),teste (i+60),
        # SVM
        teste (i+61),teste (i+62),teste (i+63),teste (i+64),teste (i+65),
        teste (i+66),teste (i+67),teste (i+68),teste (i+69),teste (i+70),
        # RPART / ANN
        teste (i+71),teste (i+72),teste (i+73),teste (i+74),teste (i+75),
        teste (i+76),teste (i+77),teste (i+78),teste (i+79),teste (i+80),
        # MAXLIKE
        teste (i+81),teste (i+82),teste (i+83),teste (i+84),teste (i+85),
        teste (i+86),teste (i+87),teste (i+88),teste (i+89),teste (i+10),
        # MAXENT
        teste (i+91),teste (i+92),teste (i+93),teste (i+94),teste (i+95),
        teste (i+96),teste (i+97),teste (i+98),teste (i+99),teste (i+100)
        # MARS
        teste (i+101),teste (i+102),teste (i+103),teste (i+104),teste (i+105),
        teste (i+106),teste (i+107),teste (i+108),teste (i+109),teste (i+110)
        )
 colnames (s) = c("ice", "depth", "salinity", "temperature")
 return (s)
}
f (0)
im <- cbind (
 mean (f(0)[,1]), #ice
 mean (f(0)[,2]), #depth
 mean (f(0)[,3]), #salinity
 mean (f(0)[,4])) #temperature
colnames (im) = c("ice", "depth", "salinity", "temperature")
```

```
im

###############################################
###############################################
##### Creating species suitability maps
### Example with Sargassum bermudense

### Calling ensemble rasters
Sbermudense.present <- raster ("Sbermudense/ensemble.bin.t10.presente_Sbermudense_maxent.default.tif")
Sbermudense.rcp45 <- raster ("Sbermudense/ensemble.bin.t10.rcp45_Sbermudense_maxent.default.tif")
Sbermudense.rcp85 <- raster ("Sbermudense/ensemble.bin.t10.rcp85_Sbermudense_maxent.default.tif")

### Plotting maps
windows()
par (mfrow=c(1,3))
{
plot (Sbermudense.present, legend=F, col=my.colors(1000))
mtext("A)", side=3, line=2, at=-120, cex=1, family="serif", font=2)
mtext("Present", side=3, line=2, at=-60, cex=1, family="serif", font=2)
mtext("S. bermudense", side=2, line=6, at=0, cex=1, family="serif", font=3)

plot (Sbermudense.rcp45, legend=F, col=my.colors(1000))
mtext("B)", side=3, line=2, at=-120, cex=1, family="serif", font=2)
mtext("RCP 4.5", side=3, line=2, at=-60, cex=1, family="serif", font=2)

plot (Sbermudense.rcp85, legend=F, col=my.colors(1000))
mtext("C)", side=3, line=2, at=-120, cex=1, family="serif", font=2)
mtext("RCP 8.5", side=3, line=2, at=-60, cex=1, family="serif", font=2)
}
```

CONCLUSÃO

Os resultados obtidos com a modelagem de nicho ecológico corroboram parcialmente nossas hipóteses iniciais. Todas as 13 espécies (12 morfoespécies e 1 espécie filogenética) de *Sargassum* analisadas tiveram manutenção ou aumento do limite latitudinal com adequabilidade ambiental propícia para a espécie. Esse aumento foi mais pronunciado no cenário RCP 8.5 do que no cenário RCP 4.5 e em direção ao norte do que em direção ao sul. Considerando que as espécies de *Sargassum* são fundadoras, essas predições sugerem que pode ocorrer um movimento de deslocamento de comunidades marinhas tropicais em direção a hábitats temperados quentes em maiores latitudes.

Contrariamente ao hipotetizado, apenas metade das morfoespécies analisadas apresentou diminuição da sua área de adequabilidade ambiental, em especial na região Equatorial e no Caribe. A outra metade apresentou aumento generalizado na sua área de adequabilidade ambiental, com aumento dessa área tanto nos pólos como em latitudes tropicais. Todas as morfoespécies tiveram o efeito em sua área de adequabilidade - seja aumento ou diminuição da área - com maior magnitude no cenário RCP 8.5 do que no cenário RCP 4.5. A espécie filogenética apresentou um ligeiro aumento de sua área de adequabilidade no cenário RCP 4.5 e uma diminuição no cenário RCP 8.5. Todas as espécies que apresentaram um aumento da área de adequabilidade ambiental incorporaram, nas predições para os cenários futuros, toda a área de adequabilidade contida no cenário presente. As espécies que tiveram sua adequabilidade ambiental diminuída não apresentaram mudanças bruscas de área em relação à predição para o presente, ou seja, suas áreas de adequabilidade futura estão dentro, em grande parte, das áreas de adequabilidade atuais.

Atenção deve ser dada a um eventual aumento das áreas de ocorrência de *S. pteropleuron* e a uma drástica redução de populações tropicais das morfoespécies *S. stenophyllum*, *S. cymosum* e *S. buxifolium*. Esforços para conservação e iniciativas de manejo e, principalmente, de pesquisas e monitoramento destas espécies devem ser mantidas e ampliadas.

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