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Lidiane Pires Gouvêa

Impactos das mudanças climáticas nas florestas marinhas e costeiras: cenário atual e perspectivas futuras

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IMPACTOS DAS MUDANÇAS CLIMÁTICAS NAS FLORESTAS MARINHAS E COSTEIRAS: CENÁRIO ATUAL E PERSPECTIVAS FUTURAS

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O presente trabalho em nível de doutorado foi avaliado e aprovado por banca examinadora composta pelos seguintes membros:

Dr. (a) Leonardo Rorig
Universidade Federal de Santa Catarina

Dr. (a) João Silva
Universidade do Algarve

Dr. (a) Sérgio Floeter
Universidade Federal de Santa Catarina

Certificamos que esta é a **versão original e final** do trabalho de conclusão que foi julgado adequado para obtenção do título de doutor em Ecologia.

_____
Coordenação do Programa de Pós-Graduação

_____
Prof. Paulo Antunes Horta Jr.
Orientador

Florianópolis, 2021.

Este trabalho é dedicado à minha família e
ao meu companheiro Nuno.

AGRADECIMENTOS

Estamos a destruir o planeta e o egoísmo de cada geração não se preocupa
em perguntar como vão viver os que vêm depois. A única coisa que importa
é o triunfo de agora. É a isto que eu chamo "cegueira da razão".

(*El Cronista*– José Saramago, 1998)

RESUMO

Iniciativas de mitigação de mudanças climáticas atraíram um grande interesse no papel dos "sumidouros naturais de carbono", particularmente nos ecossistemas marinhos costeiros. A biomassa acima do solo (AGB) representa uma parte substancial do reservatório de carbono orgânico das florestas marinhas que podem ser afetadas pelas mudanças climáticas. A importância do estudo de perdas AGB tem se tornado cada vez mais urgente, porque é a partir dela que o CO_2 atmosférico é incorporado no organismo e assim transforma-se em biomassa. Desta forma, este trabalho teve como investigar os fatores ambientais responsáveis pela variabilidade espacial da biomassa e distribuição de florestas marinhas e costeiras como aquelas estruturadas por *Sargassum* e Manguezais, sob cenários futuros de mudanças climáticas. No primeiro capítulo, nós utilizamos ferramentas estatísticas de modelagem de ocorrência e biomassa "*Boosted regression trees*" (BRT), para mostrar o importante destaque da macroalga *Sargassum* como um potencial recurso para mitigação de CO_2. *Sargassum* AGB totalizou 13,1 Pg C em escala global, o que é uma quantidade significativa de carbono e comparável a outros ecossistemas marinhos, como florestas de mangue, marismas e gramas marinhas. No capítulo 2, nós avaliamos as diferenças no ajuste ecofisiológico de *Sargassum* ao longo da costa brasileira e testamos se estes ajustes eram suficientes para a manutenção do crescimento, sob cenários futuros de aquecimento global. Nós verificamos que o *Sargassum* apresenta compostos químicos ao longo da costa brasileira impulsionados por fatores ambientais macroecológicos que também determinam províncias e ecorregiões biogeográficas. Os fatores abióticos, principalmente a temperatura nos trópicos, levam a grandes estoques de biomassa e carbono. As duas populações de *Sargassum cymosum* podem perder biomassa em conseqüência da diminuição da taxa de crescimento relativo sob estresse térmico, particularmente se o clima do planeta seguir o pior cenário RCP 6.0 e 8.5. Populações de borda como as que estão presentes em Santa Catarina apresentaram maior suceptibilidade na temperatura de 30°C, pois as taxas de crescimento passam a apresentar valores negativos, aproximadamente -1% d^{-1}. Por fim, no terceiro capítulo, nós analisamos as perdas de área e AGB nas florestas de mangues sob mudanças climáticas previstas nos cenários (RCP 2.6 e 8.5), levando em consideração temperatura e precipitação, através da modelagem estatistica BRT. As perdas potenciais de biomassa em florestas de mangue devido às mudanças climáticas variam de 5 a 14% na área e de 26 a 42% na biomassa em escala global. Isso corresponde a perdas absolutas de 8.345 a 24.212 km^2 e de 0,56 a 0,90 Pg de AGB. Nossos resultados reforçam a importância de estudos com enfoque na perda de área/biomassa e consequentemente dos serviços ecossistêmicos por ambientes marinhos. Este estudo mostra como a variação dos recursos ambientais sob mudanças climáticas podem aumentar a vulnerabilidade das espécies, principalmente das macroalgas formadoras de dossel como o *Sargassum* e florestas de mangues.

Palavras-chave: Ecossistemas marinhos; *Sargassum*; Florestas de mangues; Mudanças climáticas, Modelagem de distribuição e biomassa.

ABSTRACT

Climate change mitigation initiatives have attracted interest in the role of natural carbon sinks, particularly in coastal systems. The atmospheric CO_2 is incorporated into the organism and convert in biomass. Above-ground biomass (AGB) represents a substantial part of the organic carbon reservoir in marine forests that can be affected by climate changes. Here, we address the environmental factors responsible for the spatial variability in distribution and AGB of two important components of marine ecosystems, such as *Sargassum* and mangrove forests under climate changes. The first chapter addresses the potential role of *Sargassum* in climate change mitigation. We modelled global distributions and quantified carbon stocks as above-ground biomass (AGB) with machine learning algorithms "*Boosted regression trees*" and climate data. *Sargassum* AGB totalled 13.1 Pg C on a global scale, which is a significant amount of carbon and comparable to other marine ecosystems, such as mangrove forests, salt marshes and seagrass. In Chapter 2, we assessed the differences in *Sargassum*'s ecophysiological adjustment along the Brazilian coast, and we tested for differences in the thermal sensibility to warming between edge populations collected in tropical and warm temperate regions. *Sargassum* presents chemical compounds along the Brazilian coast driven by macroecological environmental factors that also determine provinces and biogeographic ecoregions. Abiotic factors, especially temperature in the tropics, leading to large stocks of biomass and carbon. However, the two populations of *Sargassum cymosum* could lose biomass because of the decrease in the relative growth rate under thermal stress, mainly if the planet's climate follows the RCP 8.5 scenario. Edge populations in the warm temperate region showed greater susceptibility at a temperature of 30°C, and growth rates presented negative values around -1% d^{-1}. In the last chapter, we report the potential loss of mangrove forests under contrasting scenarios of future climate change (RCP 2.6 and 8.5) by modelling global distributional and biomass shifts. Potential biomass losses in mangrove forests varied from 5 to 14% in the area and from 26 to 42% in biomass on a global scale. This corresponds to total losses of 8,345 to 24,212 km^2 and 0.56 to 0.90 Pg of AGB. Our results reinforce the importance of studies focusing on the loss of area/biomass and, consequently, on ecosystem services in marine environments. This study shows how the variation of environmental resources under climate change can increase the vulnerability of species, especially canopy-forming macroalgae such as *Sargassum* and mangrove forests.

Keywords: Marine ecosystems; *Sargassum*; Mangrove forests; Climate changes, Distribution, and biomass modelling.

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Figure 1. (a) Important marine ecosystems (from left to right: mangroves, saltmarshes, seagrasses and *Sargassum* beds). Main scheme represents carbon uptake via photosynthesis (green arrows) and subsequent long-term sequestration into biomass and

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LISTA DE ABREVIATURAS E SIGLAS

DIC	Dissolved inorganic carbono (carbono inorgânico dissolvido)
Corg	Carbono orgânico
Cinorg	Carbono inorgânico
CH_4	Metano
CCS	Carbon capture and storage
RCPs	Representative Concentration pathway (Caminhos de concentração representativos)
NDCs	Nationally Determined Contributions (Contribuições nacionalmente determinadas)
MHWs	Marine heatwaves (Ondas de calor marinhas)
GEE/GHG	Greenhouse gas (Gás de efeito estufa)
AGB	Aboveground biomass (biomassa acima do solo)
BRT	Boosted Regression trees
TgC	Teragrama de carbono
PgC	Petagrama de carbono
GtC	Gigatonelada de carbono
km^2	quilômetro quadrado
ha	Hectare
BC	Blue Carbon (carbono azul)
AIC	Aikaike´s information criterion
TSS	True skill statistics
AUC	Receiver operating characteristic curve

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1 INTRODUÇÃO GERAL

1.1 Ecossistemas marinhos e costeiros, sequestro de carbono e mitigação das mudanças climáticas

As discussões sobre aquecimento global e mudanças climáticas, mostram o papel do carbono em suas diferentes formas como protagonistas nas discussões acadêmicas e sociais. As incertezas futuras baseadas em diferentes cenários vêm sendo sistematizados e divulgados pelo Painel Intergovernamental de Mudanças climáticas (IPCC, 2014). Da mesma forma, vem crescendo a percepção de que os oceanos e seus diferentes ecossistemas marinhos costeiros absorvem boa parte do carbono liberado através da queima de combustíveis fósseis e do desmatamento. A maior parte deste carbono está sob a forma orgânica, particulada, ou ainda sob a forma mineral de carbonatos que se acumulam no fundo dos oceanos (ZHANG *et al.*, 2017). Todo esse carbono é continuamente reciclado dentro da cadeia planctônica (fitoplâncton, zooplâncton), além do nécton, que o devolve ao compartimento inorgânico via respiração (BAUER *et al.*, 2013). As trocas de CO_2 atmosférico e oceânico equivalem a 90 Gt (gigatoneladas) de carbono por ano, possibilitando o rápido equilíbrio da atmosfera com a água superficial (Fig.1).

Figura 1: Diagrama conceitual mostrando a biogeoquímica do carbono associada às trocas ar-água de CO_2. As linhas azuis indicam os processos que aumentam a captação de CO_2 atmosférico, e as linhas vermelhas indicam aqueles que aumentam a emissão de CO_2 na atmosfera. A concentração de CO_2 na água superficial é afetada pelo equilíbrio da fotossíntese, respiração e remineralização, que regula o DIC (1 e 2). Carbono orgânico dissolvido (Corg), carbono inorgânico particulado (Cinorg) e entradas de DIC de sistemas terrestres e oceanos costeiros (3 e 4). Produção de Cinorg do ecossistema líquido (o equilíbrio de calcificação e dissolução), regulando diretamente tanto DIC quanto alcalinidade total (5, 6) e temperatura (solubilidade de CO_2).
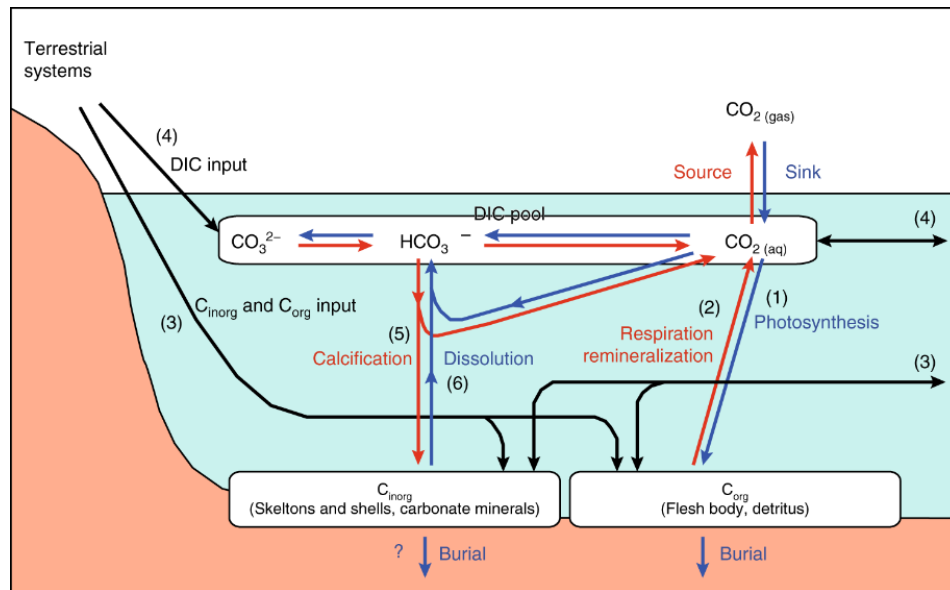
Fonte: Imagem extraída de MACREADIE *et al.,* 2019.

Os dois sumidouros mais importantes para o aprisionamento de carbono a longo prazo (após a respiração e remineralização serem considerados) são os solos terrestres e o oceano profundo, com estimativa de armazenamento total em 39.3 GtC (FARRELLY *et al.*, 2013). Tal como acontece com os solos terrestres, o carbono sequestrado nos sedimentos marinhos pode permanecer durante períodos geológicos sob a forma de carbono orgânico particulado, conhecido como carbono azul, do inglês "*blue carbon*" (BC). Os sistemas BC bem como manguezais, gramas marinhas e marismas sequestram o CO_2 atmosférico e o convertem em uma forma mais estável de carbono fixado a esqueletos orgânicos que são armazenados principalmente na biomassa dos organismos e sedimentos (MCLEOD *et al.*, 2011). Recentemente, as macroalgas marinhas, que são os produtores primários dominantes na zona costeira, também foram consideradas como contribuintes para o sequestro global de

BC, agindo como doadores de carbono para outros ecossistemas onde seu material orgânico se acumula (Hill *et al.,* 2015; Krause-Jensen e Duarte, 2016). Os sistemas de carbono azul são mais eficientes do que os terrestres no sequestro de carbono orgânico a longo prazo (Fig. 2; LAFFOLEY *et al.*, 2020; MCLEOD *et al.*, 2011). Apesar destes ecossistemas cobrirem menos de 2% de área de superfície do planeta, estudos mostram que os produtores primários marinhos, contribuem com pelo menos 50% da produção mundial de fixação de carbono e podem ser responsáveis por até 71% de todo o armazenamento de carbono em sedimentos oceânicos (NELLEMAN *et al.,* 2009; CHUNG *et al.,* 2011). Nesse sentido, estão sendo reconhecidos pelo papel essencial na mitigação de mudanças climáticas (Figura 2; FOURQUREAN *et al.*, 2012; LOVELOCK e DUARTE, 2019). Além disso, a degradação de áreas úmidas tem o potencial de liberar grandes quantidades de carbono armazenado de volta na atmosfera e na coluna de água, o que significa que a conservação e a restauração desses sistemas também podem reduzir as emissões potenciais (HOWARD *et al.,*2017).

Figura 2: Diagrama conceitual do sequestro de carbono por ecossistemas de carbono azul e algumas das atividades que influenciam a troca de CO_2 entre a atmosfera, o solo e o oceano em áreas costeiras e em mar aberto. Os principais pools globais de carbono incluem a atmosfera, oceanos, combustíveis fósseis, vegetação, solos e detritos. Aterros, chaminés, criação de gado e outras atividades humanas resultam em emissões adicionais de metano (CH_4).
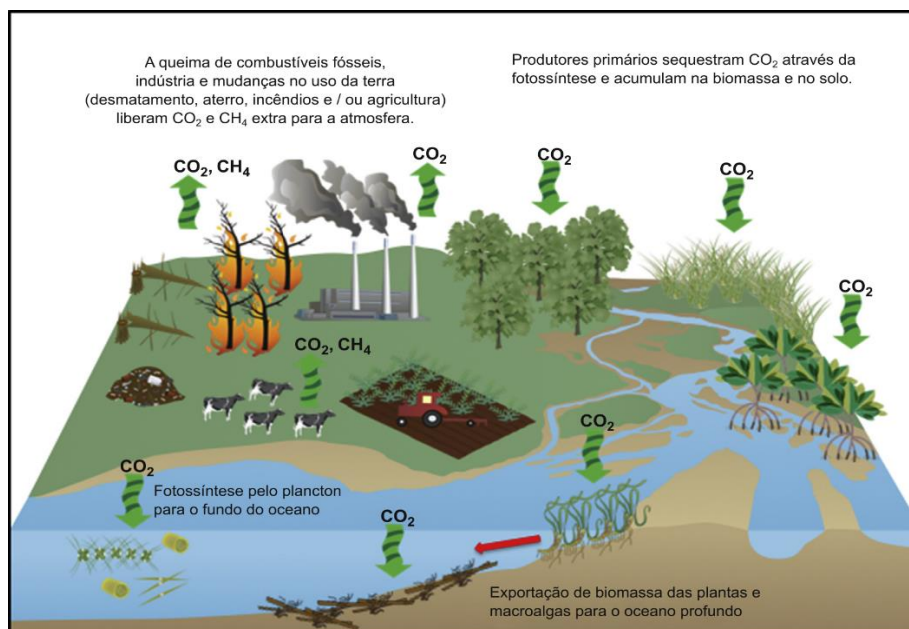
Fonte: Imagem adaptada de SERRANO *et al,.* 2019.

Marismas, manguezais, bancos de gramas marinhas e de macroalgas são ecossistemas autotróficos, que incorporam o carbono através da fotossíntese possibilitando a estruturação de fitofisionomias que alteram a paisagem costeira. Estes dosséis apresentam AGB (do inglês, "*Aboveground biomass*" ou Biomassa acima do solo) que tem complementado o entendimento sobre o balanço de carbono no nosso planeta (CEBRIAN e DUARTE, 1996). O carbono é sequestrado a curto prazo (decenal) na biomassa e em escalas de tempo mais longas (milenar) nos sedimentos (BARRÓN e DUARTE, 2015; DUARTE *et al.*, 2017). Em escala global, os ecossistemas marinhos combinados sequestram o equivalente a 500-1800 Tg de CO_2/ano. Além disso, estas zonas úmidas vegetadas apresentam sequestro anual de carbono pela AGB, entre 1% e 5% das emissões atuais de CO_2 da queima de combustível fóssil, tornando-os importantes e eficientes sumidouros de carbono quando se considera a taxa de sequestro/área (SERRANO *et al.,* 2019). Estima-se que os habitats marinhos nas zonas costeiras forneçam mais de US\$ 14 trilhões em serviços ecossistêmicos por ano, ou cerca de 43% do total global (COSTANZA *et al.,* 1997).

As florestas de manguezais sozinhas podem capturar até quatro vezes mais carbono do que as tropicais terrestres por unidade de área (Sanderman *et al.,* 2018). Sua produção primária líquida (NPP) em AGB pode variar entre ~ 11 e 19 tC ha/ano (SHERMAN; FAHEY; MARTINEZ, 2003), o que está na mesma ordem de magnitude das florestas perenes úmidas terrestres e de turfeiras (ALONGI *et al.*, 2014; MALHI ; DOUGHTY; GALBRAITH, 2011), representando 30% do sequestro de carbono dos ecossistemas costeiros (ALONGI e MUKHOPADHYAY, 2015). O NPP total de manguezais é de cerca de 200 TgC/ano (ALONGI e MUKHOPADHYAY, 2015; BOUILLON *et al.*, 2008), mas a maior parte desse carbono é perdida ou reciclada via fluxo de CO_2 para a atmosfera ou exportadas para o oceano (~ 60%). O carbono restante é responsável por entre 18,4 e 34,4 TgC/ano que é considerado um armazenamento significativo de longo prazo (ALONGI, 2014; BOUILLON *et al.*, 2008; MCLEOD *et al.*, 2011; BREITHAUPT *et al.,* 2012). Embora grande parte do carbono seja armazenado no sedimento, medidas de AGB são necessárias para a compreensão da dinâmica da ciclagem da matéria orgânica nos manguezais (SOARES e SCHAEFFER-NOVELLI, 2005).

Embora as macroalgas apresentem alta produção primária de 0,19-0,64 PgC (HILL *et al.,* 2015), taxas de fragmentação e transporte (GAO e MCKINLEY, 1994; WERNBERG

et al., 2011), além de serem reconhecidos como potenciais doadores de carbono para os sedimentos, ainda não são entendidos como "*blue carbon*". Nestes habitats de macroalgas, como florestas de kelp e *Sargassum*, o estoque de carbono está na forma de biomassa aérea. No entanto, o desprendimento das macroalgas do substrato, pode ocorrer por senescência natural, deslocamento por herbívoros (HAAVISTO *et al.,* 2017) e por forças hidrodinâmicas (BRENNAN *et al.,* 2014). Assim, passam por períodos de transporte nas águas superficiais, até eventualmente afundarem, deteriorando ou transformando-se em áreas de deposição (HYNDES *et al.*, 2014; MACREADIE *et al.*, 2017b). Na natureza, cerca de um terço da produção primária líquida por macroalgas (~ 567 TgC/ano) pode ser remineralizado (KRAUSE-JENSEN e DUARTE, 2016). No entanto a não inclusão das macroalgas como sistemas BC, dificulta sua inclusão em jurisdições nacionais claras para ações de gestão eficazes e quantificáveis. Estimativas recentes mostram que 173 TgC/ano (representando cerca de 11% da produção líquida bruta) são sequestrados por macroalgas em sedimentos de plataforma e oceanos profundos, bem como em habitats dominados por angiosperma (CHEN e XU, 2020). Esta contribuição excede o sequestro total de carbono de todas as plantas convencionais BC (Fig. 3; 111–131 TgC/ano).

Figura 3: Fluxos globais de CO_2 e "guerreiros" de carbono azul promissores para captura e armazenamento de carbono (CCS). (A) Fluxos globais de CO_2 sob perturbação por atividades antropogênicas. As setas indicam os fluxos de carbono com números em unidades de gigatonelada de carbono (GtC/ano) (médias de 2009–2018). A incorporação dos "guerreiros" de carbono azul proposto, incluindo algas cultivadas/ selvagens, microalgas e recifes de coral, é destacada em vermelho, o que pode ser antecipado para sequestrar adicionalmente mais CO_2 (seta vermelha quebrada) da atmosfera do que as plantas de carbono azul convencionais. (B) Comparação do CCS entre os guerreiros de carbono azul atuais (manguezais, marismas e ervas marinhas) e os propostos (macroalgas, recifes de coral e microalgas).
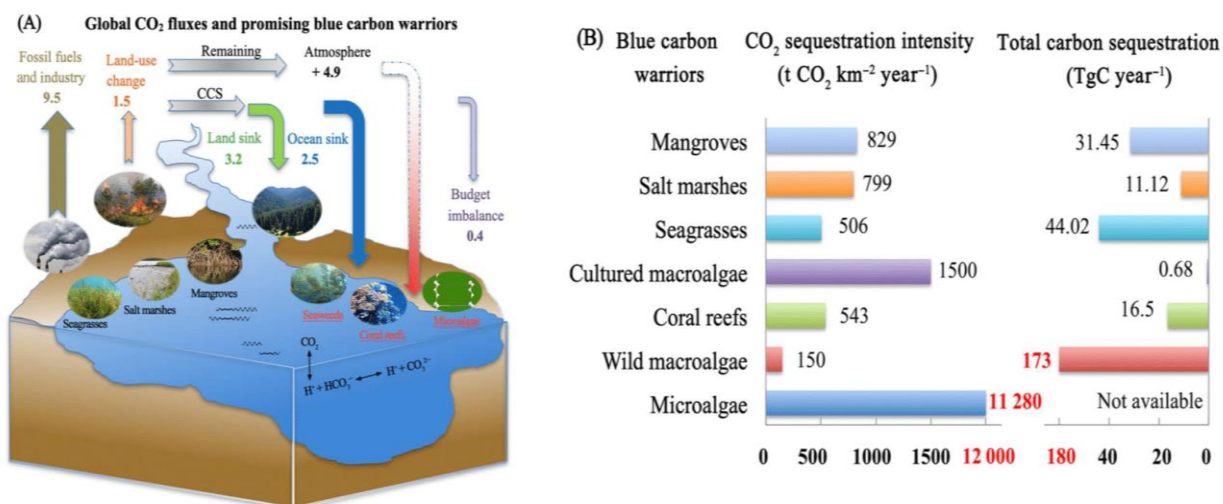
Fonte: Imagem extraída de CHEN e XU, 2020.

Além disso, a sulfatação de polissacarídeos que se observa especialmente na formação da parede celular de diferentes grupos de macroalgas proporciona o aumento da estabilidade da matéria orgânica, demonstrando a sua contribuição para estoques de carbono de longo prazo (CHUNG *et al.,* 2013; SONDAK e CHUNG, 2015; TREVATHAN-TACKETT *et al.,*2015). Registros fósseis de sedimentos marinhos mostram a presença de carbono de macroalgas de regiões polares a tropicais, em ambientes rasos e profundos, de tempos passados a presentes, demonstrando o papel evolutivo e ecológico das macroalgas no balanço global de carbono (KRAUSE-JENSEN *et al.*, 2018; ORTEGA *et al.*, 2019; QUEIRÓS *et al.*, 2019). Ainda assim, as iniciativas enfocando na contribuição de carbono azul pelas macroalgas foram realizadas apenas na China e Coreia, que incluíam habitats artificiais de carbono azul (por meio da aquicultura de algas) no Programa Nacional de Carbono Azul (CHUNG *et al.*, 2011; HILL *et al.*, 2015; SONDAK e CHUNG, 2015). A

quantidade considerável de áreas adequadas para a aquicultura global de macroalgas (~48 milhões de km^2) reforça a perspectiva de que estes produtores primários poderiam ajudar a atenuar a eutrofização, hipóxia e acidificação dos oceanos, em vários países (FROEHLICH *et al.*, 2019) contribuindo globalmente na mitigação do aquecimento do planeta induzido pelo CO_2 (GOUVÊA *et al.,* 2020).

1.2 Fatores ambientais como principais condutores das diferenças nos limites de distribuição e AGB sob mudanças climáticas

O aumento do CO_2 atmosférico é um dos problemas mais críticos enfrentados pela humanidade nas últimas décadas, pois seus efeitos são globais e irreversíveis. As principais consequências diretas são o aumento da temperatura (BINDOFF *et al.,* 2007) e a acidificação dos oceanos (LE QUÉRÉ *et al.*, 2016). Vias de concentração representativas (RCPs) são usadas para modelar projeções de emissões de gases de efeito estufa (IPCC, 2014). Elas originalmente compreendiam quatro projeções, variando de RCP 2.6 a RCP 8.5. A primeira representa um cenário em que a temperatura atmosférica está 2°C acima dos níveis pré-industriais; O RCP 4.5 e 6.0 preveem aumentos entre 2.4 e 2.8°C. O pior cenário de mudança climática é representado pelo RCP 8.5 que prevê aumento das temperaturas em 4,9°C até 2100 (IPCC, 2014). Os impactos climáticos podem ser significativamente reduzidos limitando o aquecimento a 1.5°C ao invés de 2°C, conforme proposto no RCP 2.6. Desta forma, as iniciativas do Acordo de Paris exigem ferramentas de adaptação e mitigação para reduzir os impactos das mudanças climáticas e aumentar a resiliência dos serviços ecossistêmicos (MCLEOD *et al.,* 2011). Além disso, o aquecimento global não é expresso por um aumento linear ao longo do tempo, mas sim pela forma de eventos extremos, como ondas de calor marinhas (MHWs), que têm aumentado em intensidade e frequência. No entanto, o aumento das temperaturas desencandeia em uma série de mudanças adicionais, como aumento do nível do mar, estratificação e alteração nos padrões de circulação dos oceanos, mudanças na precipitação e diminuição da extensão das geleiras (DONEY *et al.,* 2011).

As respostas fisiológicas dos organismos às mudanças climáticas se manifestaram a nível de população como mudanças na abundância, fenologia e na organização espacial (alteração nos limites de distribuição e dispersão). Condições subótimas e baixo desempenho individual podem causar redução da abundância e da produtividade da população, bem como distúrbios ambientais e redução da resiliência (HARLEY *et al.,* 2006;VERDONSCHOT *et al.,* 2012). A performance fisiológica é a principal determinante da tolerância de uma espécie à variabilidade e mudanças ambientais. Conforme o clima ou outras condições variam, os organismos respondem inicialmente com base em adaptações fisiológicas e comportamentais moldadas ao longo de sua história evolutiva (DONEY *et al.,* 2012; YAO e SOMERO, 2014). Novas condições podem ser toleráveis, permitindo aclimatação ou adaptação, ou podem ser intoleráveis, resultando em perda parcial ou completa da adequação do nicho, promovendo mudança na fenologia (tempo de eventos anuais) ou mesmo morte e extinção local, o que representa a perda de habitat e a retração da área de ocorrência da população (Fig. 4; HARLEY *et al.*, 2012; PESSARRODONA *et al.,* 2019).

Figura 4: Potenciais respostas ecológicas às mudanças climáticas. Esses efeitos imediatos levam a padrões emergentes, como mudanças na distribuição das espécies, biodiversidade, produtividade e processos microevolutivo.
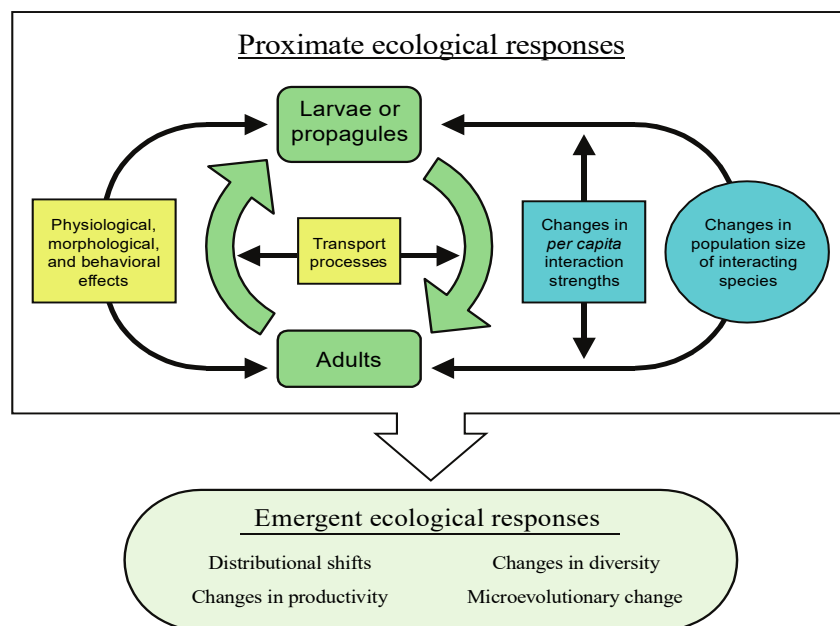
Fonte: Esquema extraído de HARLEY *et al.,* 2006.

A diferença das respostas dos organismos ao ambiente sob estresse é bastante evidente. Anomalias na temperatura, como MHWs, já provocaram perda de ~ 79% na biomassa de *Sargassum* e algas formadoras de turf, na América do Sul (Laurie, 1990). No entanto, *Avicennia germinans* que é a única espécie de mangue encontrada no norte subtropical do Golfo do México (MADRID *et al.,* 2014), deve continuar a se expandir nas próximas décadas em resposta às mudanças na frequência de temperaturas frias, precipitação e aumento do nível do mar (CAVANAUGH *et al.*, 2018; FEHER *et al.*, 2017). A vegetação dos sistemas marinhos e costeiros pode inicialmente incrementar a produtividade sob pequenos aumentos de temperatura, no entanto valores acima do ótimo térmico podem causar estresse fisiológico, com consequências negativas nas taxas de crescimento, adequabilidade ao habitat e até mesmo mortalidade (ELLISON, 2000). Uma questão chave, portanto, é se os impactos do aquecimento e do aumento da produtividade podem compensar os aumentos na respiração dos sedimentos, como no caso dos mangues (LOVELOCK e REEF, 2020). Nos últimos 50 anos, as atividades antrópicas, incluindo as mudanças climáticas, levaram ao desaparecimento de aproximadamente um terço das florestas de mangues do mundo (Valiela *et al.,* 2001) e seus serviços ecossistêmicos associados (ALONGI, 2008; DASGRUPTA e SHAW, 2013). A grande mortalidade destas florestas por causa das "secas mais longas e mais quentes" foi observada na Austrália (Golfo da Carpentaria), onde 74% dos manguezais foram perdidos. A temperatura é um importante fator que afeta o armazenamento e estoque de carbono em ecossistemas marinhos. Mudanças nos limites térmicos podem alterar os processos metabólicos de ganho e perda de carbono através da fotossíntese, respiração vegetal e microbiana. A temperatura determina o desempenho das algas marinhas nos níveis fundamentais dos processos enzimáticos e da função metabólica (COLLEN *et al.,* 2007; BISCHOF e RAUTENBERGER, 2012). Embora as macroalgas marinhas sejam geralmente adaptadas ao seu ambiente térmico, elas sofrem danos fisiológicos durante os períodos de mudanças ambientais bruscas relacionadas às ondas de calor, por exemplo (GOUVÊA *et al.*, 2017; Gurgel *et al.*, 2020).

No entanto, espécies consideradas oportunistas ou "*r*" estrategistas, muitas vezes invasoras, com maior plasticidade fenotípica, podem utilizar diferentes vetores para ocupar novas áreas e aumentar sua biomassa, como por exemplo as espécies pelágicas de *Sargassum* (SCHERNER *et al.,* 2012). Em 2011, grandes quantidades de biomassa de *Sargassum*

pelágico começaram a aparecer nas ilhas do Mar do Caribe, nas zonas costeiras da América Central e do México e na costa atlântica da África Ocidental tropical (GOWER *et al.,* 2013). No entanto, estas florações têm sido recorrentes e, por causa dos impactos socioeconômicos destas massas algas, muitos estudos se concentraram em compreender as causas destes aparecimentos (GOWER *et al.,* 2013; JOHNS *et al.*, 2020; OVIATT *et al.*, 2019; SISSINI *et al.*, 2017; WANG *et al.*, 2019). Um consenso entre os estudos é que as florações de *Sargassum* foram devidas ao aporte de nutrientes através do rio Amazonas relacionada ao desmatamento, temperaturas mais elevadas da superfície do mar, mudanças na ressurgência no noroeste da África, alterações na quantidade de deposição de poeira africana ou o sinergismo destes fatores (SISSINI *et al.,* 2017; OVIATT *et al.,* 2019; WANG *et al.*, 2019).

1.3 OBJETIVO GERAL

Investigar os fatores ambientais responsáveis pela variabilidade espacial da biomassa e distribuição de florestas marinhas e costeiras como aquelas estruturadas por *Sargassum* e Manguezais, sob cenários futuros de mudanças climáticas.

1.3.1 OBJETIVOS ESPECÍFICOS

(1) Estimar a distribuição global e biomassa do gênero *Sargassum* e quantificar seus estoques globais de carbono.

(2) Avaliar as diferenças no ajuste ecofisiológico de *Sargassum cymosum* (pigmentos fotossintéticos, metabólitos secundários, açúcar total, proteína e CN) ao longo da costa brasileira, e testar as diferenças na sensibilidade térmica entre as populações de centro e borda coletados em regiões tropicais e temperadas quentes através de experimentos laboratoriais.

(3) Estimar as mudanças globais de distribuição e AGB através de ferramentas de modelagem estatística, em florestas de mangues.

CAPÍTULO 1

GOLDEN CARBON OF *Sargassum* FORESTS REVEALED AS AN OPPORTUNITY FOR CLIMATE CHANGE MITIGATION

Golden carbon of *Sargassum* forests revealed as an opportunity for climate change mitigation

Lidiane P. Gouvêa [a, *], Jorge Assis[b], Carlos F.D. Gurgel[a], Ester A. Serrão[b], Thiago C.L. Silveira[c], Rui Santos[b], Carlos M. Duarte[d], Leticia M.C. Peres[a], Vanessa F. Carvalho[a], Manuela Batista[a], Eduardo Bastos[a], Marina N. Sissini[a], Paulo A. Horta[a]

[a] Phycology Laboratory, Department of Botany, Biological Sciences Center, Federal University of Santa Catarina, Florianopolis, Santa Catarina, Brazil

[b] CCMAR - Centre of Marine Sciences, University of Algarve, Faro, Portugal

[c] Department of Ecology and Zoology, Biological Sciences Center, Federal University of Santa Catarina, Trindade, Florianopolis, Santa Catarina, Brazil

[d] Red Sea Research Center (RSRC) and Computational Bioscience Research Center (CBRC), King Abdullah University of Science and Technology, Thuwal, Saudi Arabia

ABSTRACT

Marine climate change mitigation initiatives have recently attracted a great deal of interest in the role of natural carbon sinks, particularly on coastal systems. Brown seaweeds of the genus *Sargassum* are the largest canopy forming algae in tropical and subtropical environments, with a wide global distribution on rocky reefs and as floating stands. Because these algae present high amounts of biomass, we suggest their contribution is relevant for global carbon stocks and consequently for mitigating climate change as CO_2 remover. We modelled global distributions and quantified carbon stocks as above-ground biomass (AGB) with machine learning algorithms and climate data. *Sargassum* AGB totaled 13.1 Pg C at the global scale, which is a significant amount of carbon, comparable to other key marine ecosystems, such as mangrove forests, salt marshes and seagrass meadows. However, specific techniques related to bloom production and management, or the utilization of biomass for biomaterials, should be fostered.

Keywords: *Sargassum*; Carbon stocks; Above ground biomass; Distribution and biomass modelling; Climate change.

2.1 Introduction

Stabilizing the climate system, as envisaged under the Paris Agreement, is an enabler to achieve the United Nations Sustainable Development Goals. This agreement demands mitigation and adaptation measures to reduce climate change impacts and increase the resilience of essential ecosystem services (Damian and De Paoli, 2017; McLeod et al., 2011). In this context, ocean-based solutions for climate change adaptation and mitigation are gaining traction as a no-regrets option that had been largely overlooked in the past (Barichivich et al., 2018; McLeod et al., 2011; Sen Roy, 2018).

Carbon sequestration by photosynthetic organisms mitigates CO_2 emissions and climate change (Duarte, 2017; Gattuso et al., 2018; Khatiwala et al., 2009, see Tables S1 and S2 on the Supplementary material). Current estimates report that marine primary producer is responsible for at least 50% of global carbon fixation (54–59 Pg C year^{-1} from a total of 111–117 Pg C year^{-1}), supporting 71% of carbon storage in oceanic sediments (Chung et al., 2011; Duarte et al., 2017; Krause- Jensen and Duarte, 2016). Macroalgae represent a key component of marine ecosystems, forming marine forests that contribute about 1.5 Pg C year^{-1} of net primary production and sequester as much carbon as mangroves, salt marshes and seagrass meadows together (Krause-Jensen and Duarte, 2016). The initial debate on blue carbon overlooked the role of macroalgae, under the assumption that since they grow mainly on rocky substrate habitats, they would not contribute to carbon sequestration (Howard et al., 2017). Still, fossil records in marine sediments show the presence of macroalgae carbon from polar to tropical regions, across shallow and deep environments (Fig. 1a), and from past to present times, demonstrating the evolutionary and ecological role of macroalgae in the global carbon budget (Krause-Jensen and Duarte, 2016; Krause-Jensen et al., 2018; Ortega et al., 2019). In fact, available estimates show that >80% of the carbon produced by macroalgae can be exported to soft sediment areas (Howard et al., 2017). Compared to coastal angiosperms, recent evidence places macroalgae as global key contributors to oceanic carbon sinks (Hill et al., 2015; Trevathan-Tackett et al., 2015), which, if effectively managed, may contribute to effective climate change mitigation and adaptation (Harley et al., 2012). Still, macroalgae are not yet considered in blue carbon initiatives, with the unique exceptions for

China and Korea, which included them as artificial blue carbon habitats (i.e., through seaweed aquaculture) in the newly launched Blue Carbon National Program (Chung et al., 2011; Sondak and Chung, 2015). The considerable amount of suitable areas for global macroalgae farming (ca. 48million km^2,) could help buffer mitigate eutrophication, hypoxia, and ocean acidification, in the waters of, at least, 77 countries (Froehlich et al., 2019).

Macroalgae also form large aggregations free-floating in the ocean, epitomized by the floating pelagic *Sargassum* in the Sargasso Sea. Recently, however, exceptionally large masses of floating *Sargassum* have disrupted coastal environmental and socio-economic activities throughout the North and Southern Western Atlantic Ocean (Sissini et al., 2017; Wang et al., 2019, Laffoley et al., 2011; Ody et al., 2019). These 'golden tides' result from an increase in growth and accumulation of pelagic *Sargassum* populations (Wang et al., 2019). This particular genus comprises the largest canopy-forming algae in tropical and subtropical environments, with a wide global distribution as offshore floating rafts/populations, as well as attached forms on rocky reefs (Fig. 1a; de Széchy et al., 2012; Thiel and Gutow, 2010). Combined with their intensive carbon sequestration rates, *Sargassum* stands out as a potential add-on resource for CO_2 mitigation. However, to date no models have estimated their global extent, production, and potential immobilization of CO_2 in *Sargassum* biomass above ground. Here, we address the potential role of *Sargassum* in climate change mitigation by (1) modelling the global distribution and biomass of the *Sargassum* genus with data collected for the purpose and also from additional published studies, and (2) quantifying its global carbon stocks.

Marine ecosystem Realm	Mangrove	Salt marsh	Seagrasses	*Sargassum* Floating Atlantic	*Sargassum* Floating Global		*Sargassum* Benthic Global		*Sargassum* Combined Global
Geographic extent [10^4 km^2]	13.80-15.20	2.20-40.00	17.70-60.60	227.89	305.95	+	139.59	≈	445.54
Above ground biomass [Gg km^{-2}]	1.66-62.70	0.07-30.00	0.0002-1.58	8.25	8.25	+	0.14	≈	8.40
Carbon stock * [PgC]	5.61-6.18	0.57-10.36	4.26-8.52	7.52	10.10		0.07		13.10

* Mean global estimate

Fig. 1. (a) Important marine ecosystems (from left to right: mangroves, saltmarshes, seagrasses and *Sargassum* beds). Main scheme represents carbon uptake via photosynthesis (green arrows) and subsequent long-term sequestration into biomass and soil (brown dashed arrows) or respiration (green arrows). The *Sargassum* biomass (floating and benthic) can sequester and transport atmospheric carbon into the deep ocean. (b) Carbon storage potential of important marine ecosystems, including *Sargassum* stock. Geographic extent in Millions of hectares (10^4 km^2), Above ground biomass (Gg km^{-2}) and Mean global estimate of carbon stock in above ground biomass (PgC). Data obtained from Howard et al., (2017), except for above ground biomass values (Fourquean et al., 2012; Quintana-Alcantara et al., 2014; Rovai et al., 2016; Castillo et al., 2010). The results obtained in the present study are represented in bold. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article). The images referring to mangrove trees, seagrasses, tidal marsh, benthic and floating *Sargassum* were obtained from the websites: http://gratispng.com; belvil2009.blogspot.com and atricolinabiologa.blogspot.com.

2.2 Materials and methods

We collected *Sargassum* samples to estimate above-ground biomass (AGB) in eleven sites along the Brazilian coast, corresponding to Piauí (PI), Ceará (CE), Rio grande do Norte (RN), Pernambuco (PE), Paraíba (PB), Alagoas (AL), Bahia (BA), Espírito Santo (ES), Rio de Janeiro (RJ), São Paulo (SP) and Santa Catarina (SC) sites (Tables S3–S5 on the Supplementary material). These records are presented in Figs. S2a and S3a on the Supplementary material. The coordinates were verified from each sampling site through by GoogleEarth® (version 7.3.2.5491). Collections occurred from February to March of 2015 2016 and 2017. On average, fifteen squares of 0.0625 m2 were scraped in each site, totalizing 189 samples (Table S3 on the Supplementary material. To encompass spatial variability, squares were placed haphazardly within a transect 20 m long, on inner the *Sargassum* beds at the intertidal zone, during low tides, avoiding the edge effect. Algal samples were transferred to plastic bags and brought to the Phycology Laboratory, at University Federal of Santa Catarina (Florianopolis, Brazil). The *Sargassum* species identification was defined according to Camacho et al. (2015) for many morphotypes that are grouped into a polytomy in the S. section *Sargassum* clade (Camacho et al., 2015).

In the laboratory, we washed samples with seawater to remove sand, epifauna and epiphytes from macroalgae thalli. The encrusted epiphytes were removed with the help of tweezers. *Sargassum* samples were dried at 60 °C (± 2 °C) for 48 h. Dry weight (DW) was measured using an analytical balance (Marte, AY 220). We selected ten samples from each site for % Carbon elemental analyses.

2.2.1 Chemical analyses

Sargassum samples (0.1 g) were lyophilized, then acidified in pH 2 to remove inorganic carbon using 37% HCl for 1 min. Samples were neutralized with 0.1 M NaOH for 24 h and placed in a desiccator. Total organic matter (TOM) of above-ground biomass was estimated using High Temperature Combustion (HTC) at 450 °C for 5 h. Content of organic carbon and nitrogen were estimated using an elemental analyzer (ECS 4010, Costech Analytical Technologies, Inc., Valencia, California). The final dry weight was measured and compared to the initial weight. We considered these residuals as TOM. For elemental

analysis, each sample was placed in thin tin sheets (Lüdiswiss Sn 98, d 9/10 mm). We used %Carbon (% C) to calculate the mean global estimate of carbon stock. The %C analyzed was used in other environments, such as mangroves, tidal marshes and seagrasses (Wahyudi et al., 2016; Worm et al., 2000; Warren et al., 2012). The final value was obtained according to the equation below: Carbon stock in above−ground biomass:

Carbon stock in above-ground biomass (Pg C) = % C (dry weight) x AGB (dry weight) x area

(obtained in the Boosted Regression Trees-BRT Model)

* Dry weight was 10% of wet weight of biomass

2.2.2 Bibliography data

The main objectives of our literature review were to retrieve all studies reporting *Sargassum* aboveground biomass (AGB) and % Carbon around the world. This dataset included published peer-reviewed articles, books and book chapters (see Tables S3–S5 on the Supplementary material). A literature search was performed primarily online (Science Direct, Google Scholar and Scielo) using broad search terms such as "*Sargassum*", plus "above-ground biomass", "AGB", "carbon", "% Carbon", "productivity", "South Atlantic", "South America", "Central America", "North Atlantic", "Europe", "Africa", "Asia", "Oceania". Several searches were performed in English, Spanish and Portuguese languages (Sissini et al., 2017; Wang et al., 2019; Lapointe, 1995; Camacho and Hernández-Carmona, 2012; Pacheco-Ruíz et al., 2009; Cruz-Ayala et al., 1998; Santelices, 1977; Engelen et al., 2005; Russo, 1990; Wanders, 1976; Trono Jr and Tolentino, 1993; Ragaza and Hurtado, 2004; Wong and Phang, 2004; Gillespie and Critchley, 2011; Hoang et al., 2016; Vuki and Price, 1994; Fulton et al., 2014; Parr, 1939; Howard and Menzies, 1969; Butler and Stoner, 1984; Sembera et al., 2018; Atkinson and Smith, 1983; Hanson, 1977; Oyesiku and Egunyomi, 2014; Chen and Yang, 2005).

2.2.3 Statistical analyses

To estimate *Sargassum* occurrence and biomass for the whole world, we compiled additional data of *Sargassum* above-ground biomass (AGB) and % Carbon from literature

(Tables S3–S5 on the Supplementary material). Distribution and AGB models for floating and benthic *Sargassum* species were performed independently. Different environmental variables were selected according to biological relevance for *Sargassum*. Seven environmental benthic data layers were used for benthic *Sargassum* species and eight environmental surface data layers were used for floating *Sargassum* species (Table S6 on the Supplementary material). We accessed variables from Bio-ORACLE (Assis et al., 2017; Tyberghein et al., 2012; see Table S6 on the Supplementary material), a dataset of marine layers for ecological modelling at a spatial resolution of 30 arcmin (~9.2 km at the equator). Considering the known vertical distribution of benthic *Sargassum* species, the layers were delimited to a maximum depth of 100 m, using a bathymetric dataset (Fig. S1).

Georeferenced presence data for the whole distribution of *Sargassum* species were compiled from the Virtual Database, Global Biodiversity Information Facility (GBIF, 2018), and several biodiversity information facilities and the available literature. These data were gridded to the spatial resolution of environmental data, and overlapped occurrences were discarded to reject duplication. To further reduce the effect of spatial autocorrelation in the models, the correlation of environmental variables within the range of occurrence records was determined as a function of geographic distance with Mantel tests (Figs. S2a and S2b on the Supplementary material) (Segurado et al., 2006). Pseudoabsences were generated randomly throughout the whole study areas, except in the localities where the species occur, in order to accurately isolate the different contribution of variables (Cerasoli et al., 2017). For floating *Sargassum*, the area was calculated to the Atlantic Ocean and worldwide. The area of Atlantic Ocean was calculated through a polygon that has these upper limits: Canada-Quebec (North America) and Portugal-Porto (Europe), while the lower limits are Brazil-Paraíba (South America) and Ghana-Accra (Africa) (Fig.S3).

Multicollinearity between environmental variables was verified through the Variance Inflation Factor (VIF). Ensemble modelling was performed by averaging the result of independent models fitted with one of the variable pairs showing high correlation (Pearson's r > 0.85; Figs. S4 and S5 on the Supplementary material).

Models explaining and predicting the potential distribution and above-ground biomass (AGB) of *Sargassum* beds were developed using a delta-lognormal statistical approach. This fitted environmental predictors against the distribution of *Sargassum*

separately from biomass and combined both methods with a product function (McGill et al., 2007). The machine-learning algorithm Boosted Regression Trees (BRT) was used since it handles non-linear relationships and complex interactions while avoiding overfitting by forcing predictors to have positive or negative monotonic responses on the models, and by optimizing the number of trees, tree complexity (TC) and learning rate (LR) (Elith et al., 2008). To obtain models with lower deviance, twenty-four combinations of parameters were tested (TC = from 1 to 6 and LR = 0.01,0.005,0.001,0.0005). A cross-validation framework using independent latitudinal bands was implemented to tune these two parameters. BRTs fitted a "Bernoulli" for and "Gaussian" distributions for occurrence and biomass, respectively. Final predictions using optimal parameters were reclassified to binomial responses, and their final accuracy was reported with True skill statistics (TSS). The area of the receiver operating characteristic curve (AUC) was used to assess the performance of distribution model while deviance explained was used for biomass model. The ecological significance of both models was investigated by determining the contribution of each environmental predictor to their performance. Finally, the area in km2was obtained through the biomass models. The BRT approach was implemented using "gbm" package (Elith et al., 2008). All analyses were performed in R (R Development Core Team, 2016) on RStudio v.3.6.6 (R. Studio Team, 2016). All maps were edited in QGIS (QGIS Development Team, 2019).

2.3 Results

We gathered 339 and 724 occurrence records of floating and benthic species, respectively. The biomass data collected in this study was complemented with the literature, in a total of 34 and 204 records of floating and benthic species, respectively (Figs. 2a and 3a). The distribution and biomass models displayed high performances (TSS 0.88–0.89, AUC 0.93–0.99, Fig. 2), showed little deviation between observations and predictions (Deviance Explained 0.75–0.80) and matched the known distribution of the genus (Figs. 2 and 3). A combination of physiologically meaningful predictors explained the distribution of *Sargassum*. Iron, maximum temperature and phosphate were particularly important for floating *Sargassum* (relative contributions >15%; Fig. 4a), while light at the bottom, salinity, maximum and minimum temperatures were important for benthic ones (relative contributions

>15%; Fig. 4b). Biomass variation for floating *Sargassum* was mostly explained by Phosphate, Iron, minimum temperature, and Salinity (Fig. 4a), while for benthic *Sargassum*, minimum temperature and Nitrate were particularly important (Fig. 4b). The combination of both distribution and biomass models predicted a suitable niche area of $227.89 \cdot 10^4 \, km^2$ and a potential standing stock $8.25 \, Gg \, km^{-2}$ of floating *Sargassum* in the Atlantic Ocean. At the global scale, models estimated 305.95 and $139.59 \cdot 10^4 \, km^2$ of floating and benthic *Sargassum*, respectively ($445.54 \cdot 10^4 \, km^2$ in total), and overall biomass of $8.40 \, Gg \, km^{-2}$, which corresponds to $13.1 \, Pg \, C$ globally (Fig. 1b).

2.4 Discussion

The potential carbon stock of *Sargassum* as a whole (i.e., benthic and floating forms) encompasses $13.10 \, Pg \, C$ globally, which is in the same order of magnitude as the global estimates for salt marshes ($10.36 \, Pg \, C$), and up to twice those available for mangroves and seagrasses (6.2 and $8.5 \, Pg \, C$, respectively). *Sargassum* can cover up to $445.54 \, 10^4 \, km^2$, which is up to 4 times more area than these ecosystems combined (Fig. 1b). The global importance of *Sargassum* is further highlighted when contrasted to additional estimates for important marine kelp forests $\sim 2.35 \cdot 10^4 \, km^2$, around 1% of *Sargassum* area (Howard et al., 2017). These values reveal that *Sargassum* aquaculture, natural stock management and restoration can represent important allies in the urgent need for CO_2 mitigation. However, without appropriated management, beached *Sargassum*, especially in the Caribbean, has afflicted fisheries and tourism, resulting in ecological and public health problems, as well as lost revenues and unanticipated remediation costs. The *Sargassum* Management Brief (Hinds et al., 2016; Milledge and Harvey, 2016; Laffoley et al., 2011) proposed some strategies to deal with these massive accumulations of algae resulting from the mass blooms. However, little attention has been focused on their role in carbon stock preservation. Techniques related to deep-sea carbon burial or the utilization of biomass for biomaterials that preserve carbon (i.e. as paper production) should be fostered.

The broad areas predicted for *Sargassum* match known distributions (Figs. 2a and 3a) and, can be explained by the high phenotypic plasticity (tolerable thermal range: 17–31 °C; Fig. 4) and efficient long-distance dispersal. Pelagic species like *Sargassum natans* have wide distributions reported from the African and European Atlantic coasts, including

Australia, New Zealand, and the southeast and southwest coasts of Asia (Guiry and Guiry, 2018). *Sargassum fluitans*, another widespread pelagic species with an alleged more restricted distribution, has been reported from the Atlantic Ocean to southeast and southwest Asia (Van den Hoek, 1987).

a
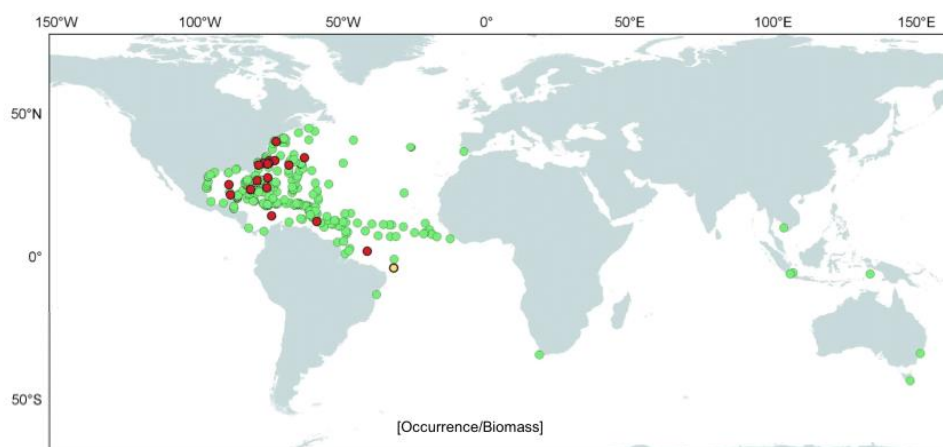
b
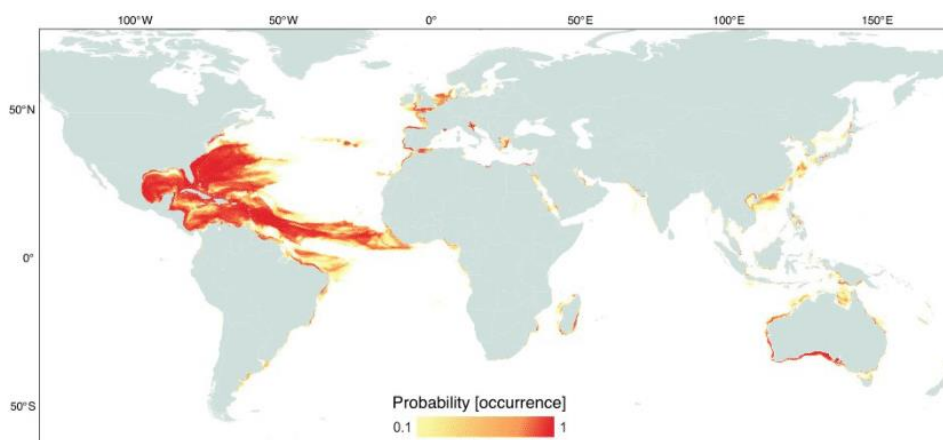
c
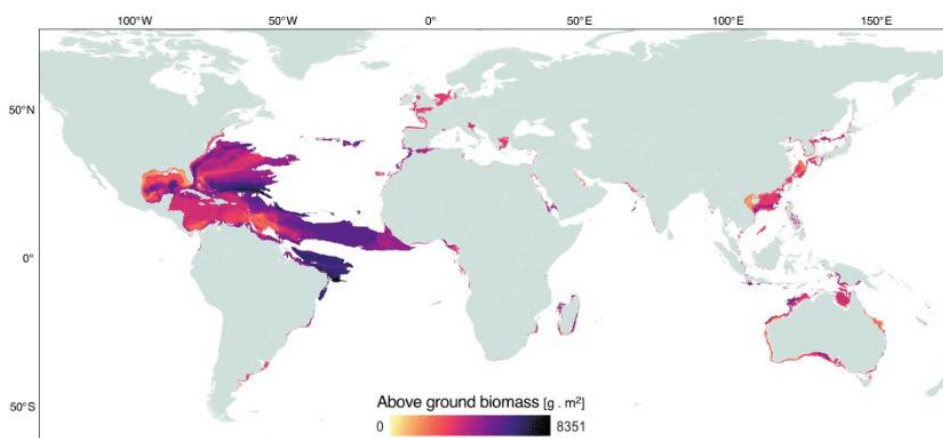
Fig. 2. (a) Records of occurrence and biomass of floating *Sargassum*. Circles depict occurrence (in green) and biomass (in red) data from literature, while yellow circle refer to data collected in this study. (b) Potential global distribution of floating *Sargassum* and (c) biomass ($g \cdot m^{-2}$) shown on a yellow (low suitability/biomass) to purple (high suitability/biomass) scale. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

a

b

Probability [occurrence]
0.1   1

c

Above ground biomass [g . m²]
0   778
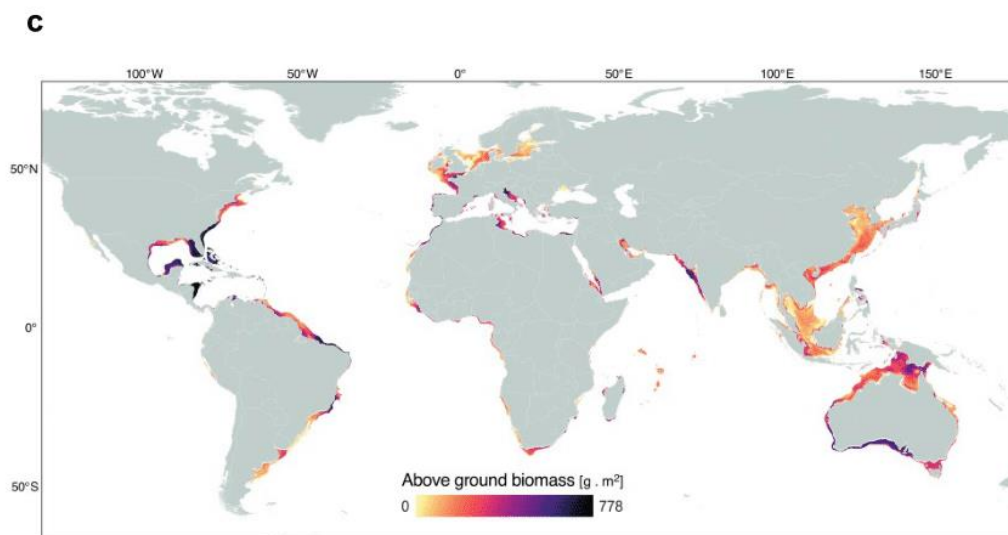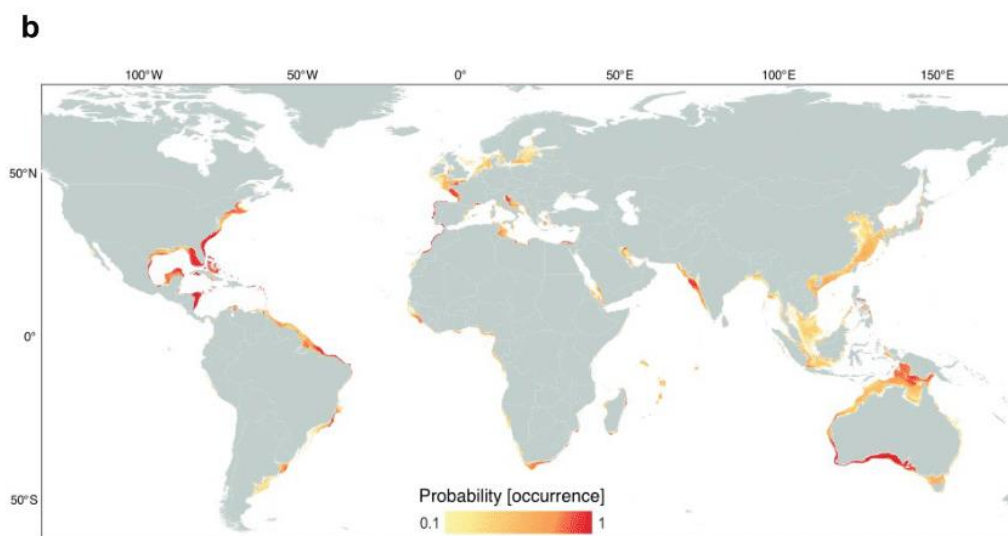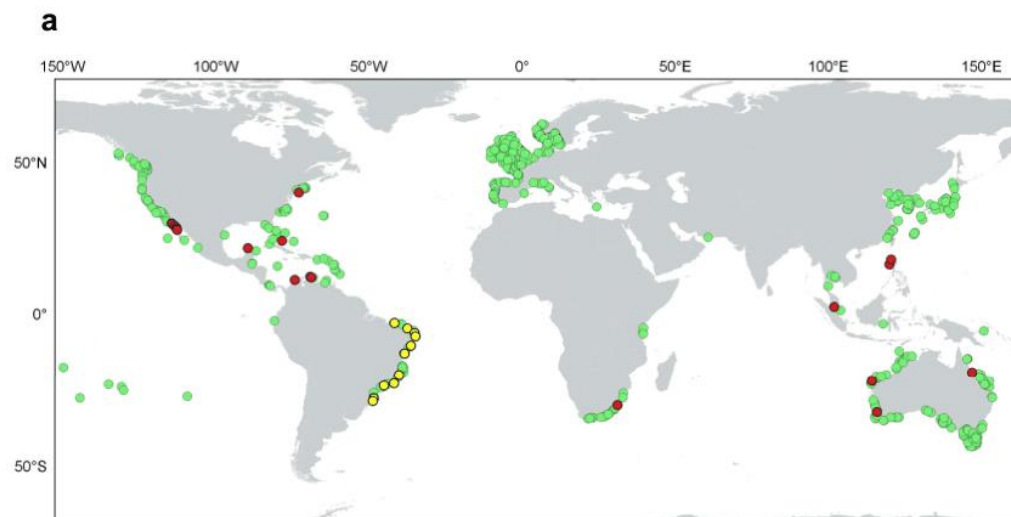
Fig. 3. (a) Records of occurrence and biomass of benthic *Sargassum*. Circles depict occurrence (in green) and biomass (in red) data from literature, while yellow circles refer to data collected in this study. (b) Potential global distribution of benthic *Sargassum* and (c) biomass (g·m^{-2}) shown on a yellow (low suitability/biomass) to purple (high suitability/ biomass) scale. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

a

Predictor	Distribution model (occurrence) Relative contribution (%)	Threshold	Biomass model Relative contribution (%)	Threshold
Iron (µmol.m^{-3})		0.001		0.001
Temp. max. (°C)		31		31
Phosphate (µmol.m^{-3})		0.1		0.1
Salinity (PSS)		20		20
Temp. min. (°C)		18		20
Nitrate (µmol.m^{-3})		0.1		1
PAR (E.m^{-2}.day^{-1})		32		10

b

Predictor	Distribution model (occurrence) Relative contribution (%)	Threshold	Biomass model Relative contribution (%)	Threshold
Light (E.m^{-2}.day^{-1})		32		31
Salinity (PSS)		35		29
Temp. max. (°C)		29		31
Temp. min. (°C)		17		20
Nitrate (µmol.m^{-3})		0.1		0.1
Phosphate (µmol.m^{-3})		0.01		1
Iron (µmol.m^{-3})		0.001		0.001
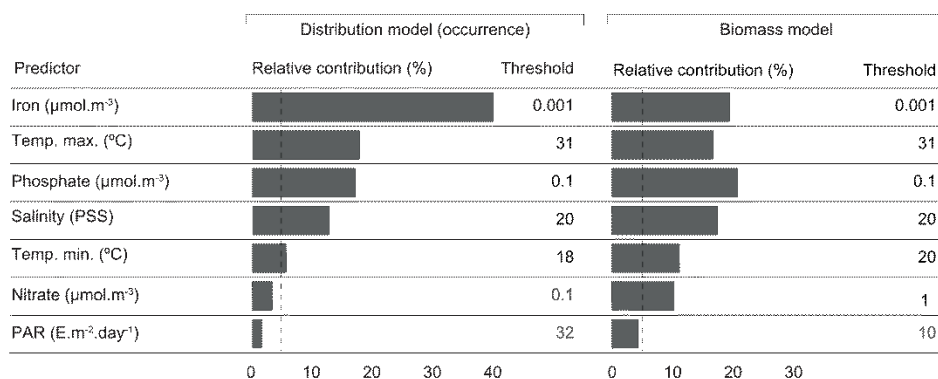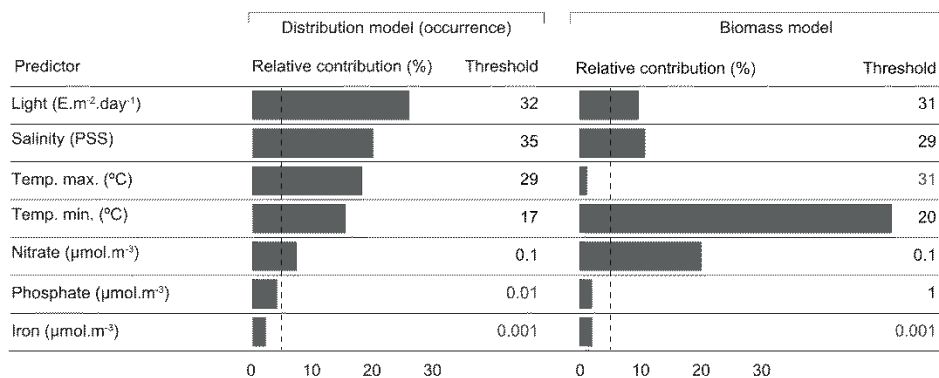
Fig. 4. Relative contribution (%) and threshold of climate variables used to model the potential distribution of (a) floating and (b) benthic *Sargassum*. Dotted lines depict contributions >5%.

The biomass predictions for *Sargassum* are in line with previous studies that reported estimates of ~7 · 10^3 Gg of floating biomass in the Gulf of Mexico and the Western Atlantic Ocean in 2005 (Gower and King, 2008), and ~20 · 10^3 Gg from West Africa to the Gulf of Mexico in June 2018, when it had the highest productivity (Wang et al., 2019). For both Atlantic regions mentioned above, our models predicted similar biomass values of 6.8 · 10^3 and 18.8 · 10^3 Gg, respectively. These floating *Sargassum* estimates are increased up to 25,2 · 10^3 Gg when considering the potential global distribution of the genus (Fig. 1b). The modelled parameters driving *Sargassum* distribution, and biomass (i.e., extreme temperatures, limiting light and nutrient thresholds) are also supported by empirical evidence (Lapointe, 1995). Studies focused on thermal, salinity and irradiance limits for species of *Sargassum* show tolerance ranges of 18°C–30°C, >20 PPT and 9.2–184.0 E·m^2·day^{-1}, respectively (Hanisak and Samuel, 1987; Li et al., 2019; Paula, 1994; Zou et al., 2018). These limits match the thresholds inferred by our models (see Fig. 4). The integration of light in the modelling seemed particularly important to set realistic vertical limits for benthic species. Benthic *Sargassum* species are known to thrive from the low intertidal down to 120 m, a range of depths mimicked by our modelling approach (Fig. S1 on the Supplementary material, De Wreede and Jones, 1973). The predictor with the highest relative influence on the distribution of pelagic *Sargassum* was iron, with a relative contribution to the models of ~41%. Such an influence could be explained by the runoff of one of the worlds' largest iron ore mining, that flows to the Amazon mouth (Nassar et al., 2002). Experiments have indicated that in limited conditions, iron-ore particles produce a fertilizer effect boosting the growth of *S. vulgare* (Nassar et al., 2002). Additional evaluations revealed a maximum *Sargassum* growth rate in chelated iron-enriched treatments (saturation of 4.3 µg/L) in different stages of the life cycle, associated with increased chlorophyll synthesis (Miki et al., 2016; Nagai et al., 2014). A consequence of this iron effect is that runoffs, combined with the growing deforestation and agriculture-related erosion, and the potential increased iron from Saharan dust (Sonter et al., 2017; Johnson et al., 2012), are all possible drivers for *Sargassum* biomass blooms. The Saharan supply of nutrients (iron and phosphate) has been

correlated with the intensification of fertility in terrestrial ecosystems (e.g., Amazon forest; Djakouré et al., 2017).

Ocean currents have a further role in shaping the distribution of floating forms. Large scale ocean transport creates the Sargasso Sea, with floating aggregations displaced towards Brazil and Africa, where the North Equatorial Recirculation Region (NERR) is located, and where parts of the currents from the Caribbean, Gulf of Mexico, and Africa converge. In this region, *Sargassum* grows and is latter redistributed to the Caribbean region with the help of the trade winds and the Brazilian Current (Wang et al., 2019). The central Atlantic region represents a marine deposit of drifting organisms that grow during their passage by the coastline. The productivity of *S. natans* is nutrient limited in oceanic waters, but it is significantly enhanced in North American coastal waters (Lapointe,1995). Benthic *Sargassum* is considered a resilient system (Loffler and Hoey, 2018), but anthropic pressure such as eutrophication may decrease population sizes (Coelho et al., 2000) and lead to local extinctions (Scherner et al., 2012). *Sargassum* communities exposed to high urbanization levels reduce photosynthetic efficiency and may be replaced by other macroalgal species typical of impacted and eutrophic environments such as *Ulva* spp., *Bryopsis* spp. and *Chondracanthus acicularis* (de Vasconcelos et al., 2019; Phillips and Blackshaw, 2011; Terawaki et al., 2003). In the same way, macroalgal losses due to climate change are a major concern. *Sargassum* populations are declining globally and, in many places, have been completely extirpated along urbanized areas of Europe, North America, Japan, Australia and Brazil (Thibaut et al., 2005; Airoldi et al., 2014). Together with global climate change and local eutrophication pressure, sedimentation, increased turbidity, overgrazing and competition with recently arrived exotic species (Airoldi et al., 2014; Connell et al., 2008; Mineur et al., 2015), they represent additional stressors that threat *Sargassum* population size, density, distribution, biomass, and their potential for carbon stock.

2.5 Conclusion

This study showed that *Sargassum* has the potential to make ecologically meaningful contributions towards golden carbon storage, with a major role in the global balance. In addition, our models can help to predict the high suitability for blooming locations of floating *Sargassum* forms through global distribution model to create strategies for managing

biomass. The better understanding of environmental drivers of *Sargassum* growth and accumulation, with the rise of Iron as an important trigger of the observed abundance, provide new paths for *Sargassum* management or production. The broad inferred distribution, spanning across the global ocean, and the high biomass levels matching empirical data, reinforce the need for transnational discussions regarding the management of carbon sequestration by macroalgae. The urgent demand for CO_2 mitigation and the threats of growing coastal urbanization represent arguments to standout benthic and floating *Sargassum*, as a primary target for conservation, management, and eventual restoration initiatives in a global context.

2.6 Funding

2.7 CRediT authorship contribution statement

Lidiane P. Gouvêa: Conceptualization, Investigation, Formal analysis, Data curation, Writing - original draft, Writing - review & editing. Jorge Assis: Methodology, Data curation, Formal analysis, Writing – review & editing, Resources. Carlos F.D. Gurgel: Investigation, Writing -review & editing. Ester A. Serrão: Writing - review& editing, Resources. Thiago C.L.

Silveira: Data curation, Writing - review & editing. Rui Santos: Writing - review & editing, Resources. Carlos M. Duarte: Writing - Review & editing. Leticia M.C. Peres: Writing – review & editing. Vanessa F. Carvalho: Writing - review & editing. Manuela Batista: Writing – review & editing. Eduardo Bastos: Writing - review & editing. Marina N. Sissini: Writing - review & editing. Paulo A. Horta: Conceptualization, Writing - review & editing, Funding acquisition, Resources.

2.7.1 Declaration of competing interest

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

2.8 Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.scitotenv.2020.138745.

(These data are presented below)

2.8.1 Supplementary Material (Figures S1-S5)

Golden carbon of *Sargassum* forests revealed as an opportunity for climate change mitigation

Lidiane P. Gouvêa[a*], Jorge Assis[b], Carlos F.D. Gurgel[a], Ester A. Serrão[b], Thiago C.L. Silveira[c], Rui Santos[b], Carlos M. Duarte[d], Leticia M.C. Peres[a], Vanessa F. Carvalho[a], Manuela Batista[a], Eduardo Bastos[a], Marina N. Sissini[a], Paulo A. Horta[a].

Affiliations:

[a] Phycology Laboratory, Department of Botany, Biological Sciences Center, Federal University of Santa Catarina, Florianopolis, Santa Catarina, Brazil.

[b] CCMAR - Centre of Marine Sciences, University of Algarve, Faro, Portugal.

[c] Department of Ecology and Zoology, Biological Sciences Center, Federal University of Santa Catarina, Trindade, Florianopolis, Santa Catarina, Brazil.

[d] Red Sea Research Center (RSRC) and Computational Bioscience Research Center (CBRC), King Abdullah University of Science and Technology, Thuwal, Saudi Arabia.

[*]Corresponding author:

Lidiane Pires Gouvêa

E-mail address: lidi_pel@hotmail.com

Figure S1: Histogram with the frequency of suitable habitats (potential distribution model) for benthic *Sargassum* as function of depth.
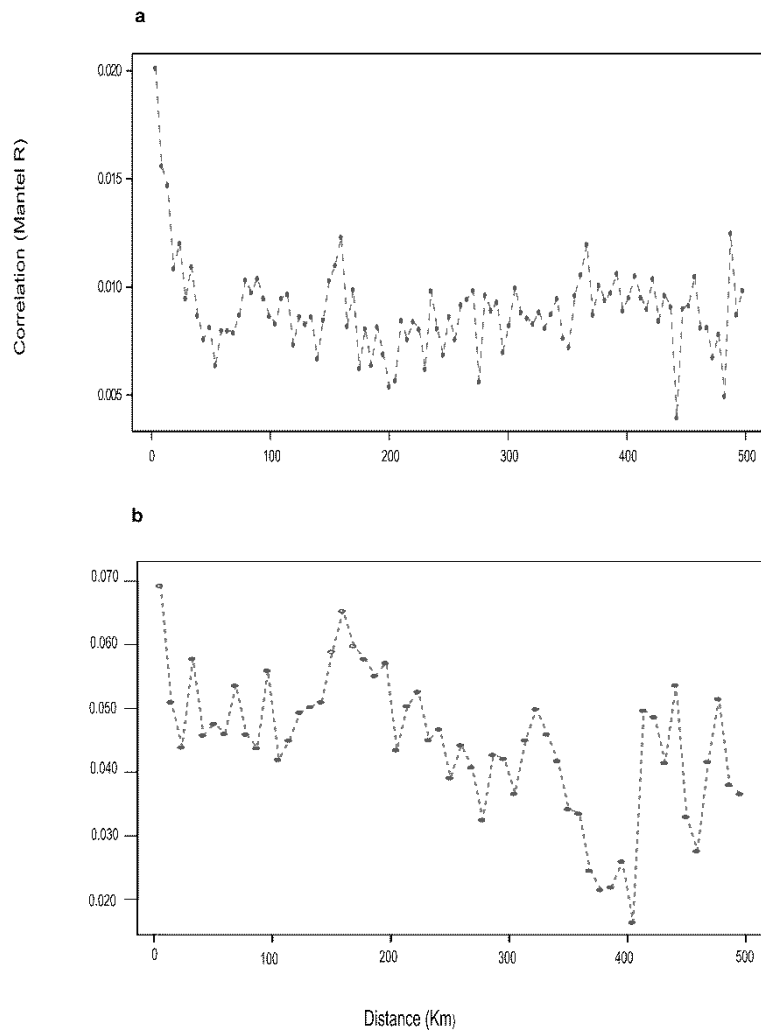
Figure S2: Spatial autocorrelation in occurrence for the (**a**) floating and (**b**) benthic

Sargassum. Significant autocorrelation is indicated by closed circles.
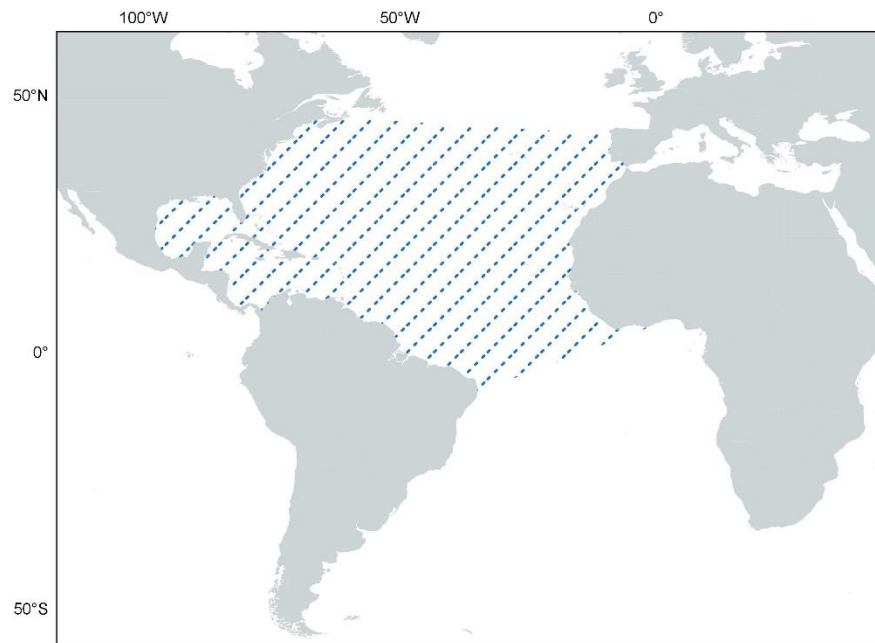
Figure S3: Polygon drawn in QGIS to measure the occupied area in Atlantic Ocean by floating *Sargassum* represented to blue dashed lines. The polygon has these upper limits: Canada-Quebec (North America) and Portugal-Porto (Europe), while the lower limits are Brazil-Paraíba (South America) and Ghana-Accra (Africa).
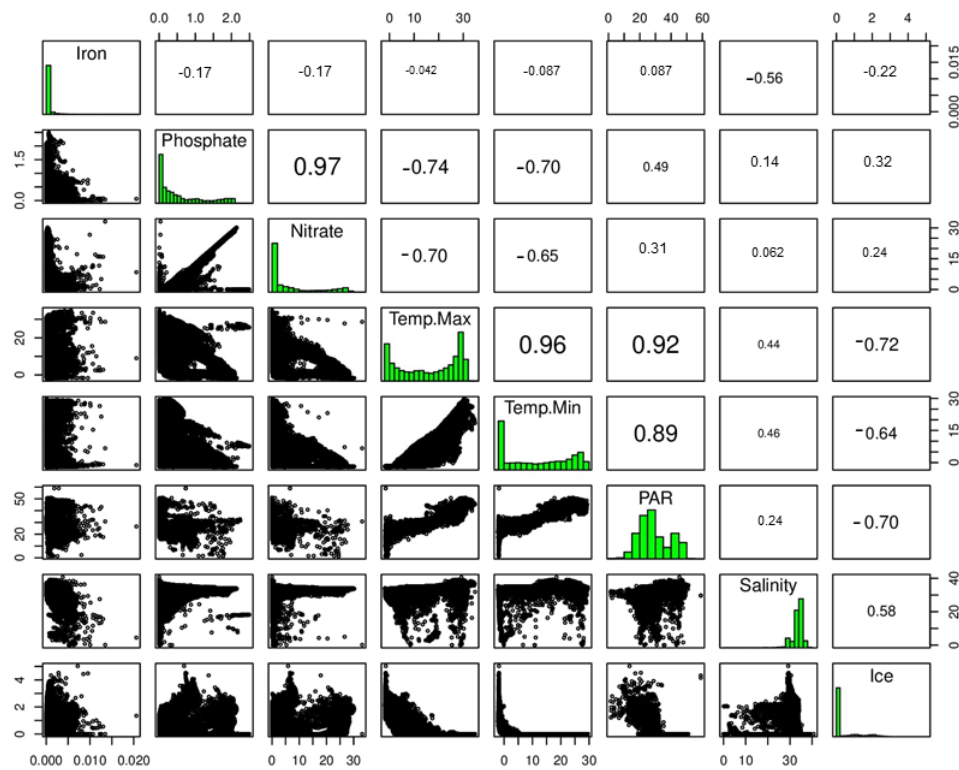
Figure S4: Histogram and pair plots of environmental variables utilized in niche modeling of floating *Sargassum*. The numbers indicate correlations between variables; the coefficient's font size is proportional to correlation strength.
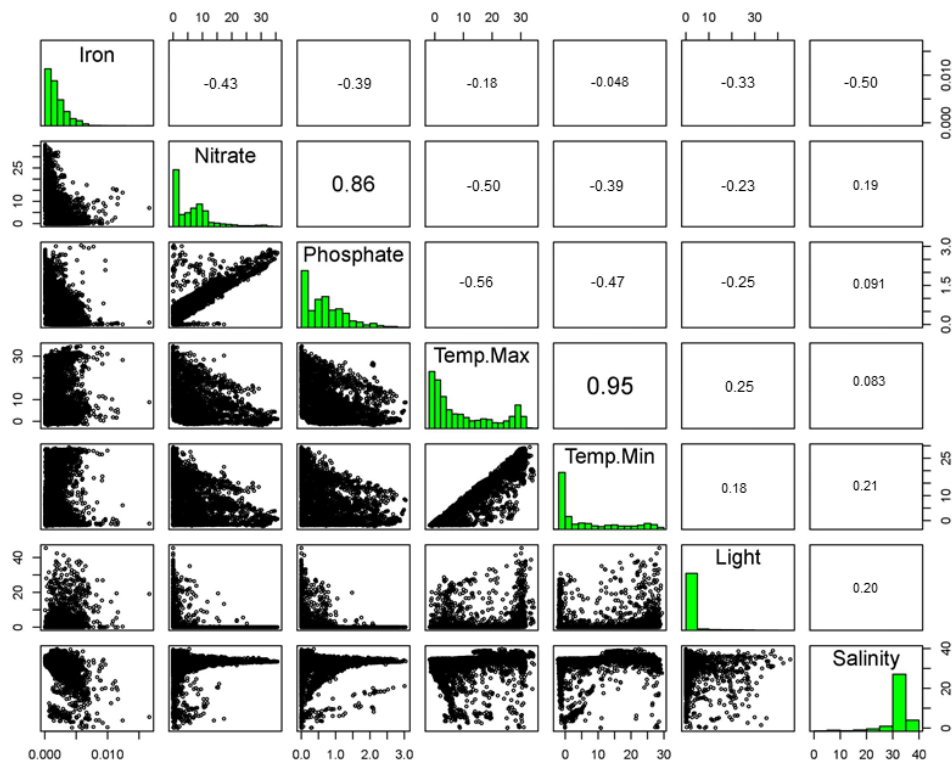
Figure S5: Histogram and pair plots of environmental variables utilized in niche modeling of benthic *Sargassum*. The numbers indicate correlations between variables; the coefficient's font size is proportional to correlation strength.

2.8.2 Supplementary Material (Tables S1-S6)

Golden carbon of *Sargassum* forests revealed as an opportunity for climate change mitigation

Lidiane P. Gouvêa[a*], Jorge Assis[b], Carlos F.D. Gurgel[a], Ester A. Serrão[b], Thiago C.L. Silveira[c], Rui Santos[b], Carlos M. Duarte[d], Leticia M.C. Peres[a], Vanessa F. Carvalho[a], Manuela Batista[a], Eduardo Bastos[a], Marina N. Sissini[a], Paulo A. Horta[a].

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[d] Red Sea Research Center (RSRC) and Computational Bioscience Research Center (CBRC), King Abdullah University of Science and Technology, Thuwal, Saudi Arabia.

[*]Corresponding author:

Lidiane Pires Gouvêa

E-mail address: lidi_pel@hotmail.com

Table S1: Potential carbon accumulation (t) and potential CO_2 sequestration (t) in 2013 for wild seaweed (Korean beds).

Specie	Carbon accumulation (t)	Potential CO_2 sequestration (t)
Eisenia/Ecklonia	116,882.30 (2.17 t·ha^{-1})	428,958.03 (7.97 t CO_2·ha^{-1})
Saccharina	69,989.40 (1.30 t C·ha^{-1})	256,861.10 (4.77 t CO_2·ha^{-1})
Sargassum	323,028.00 (**6.00 t C·ha^{-1}**)	1,185,512.76 (**22.02 t CO_2·ha^1**)

Table taken from Sondak et al., 2015

Table S2: Productivity values (g m^{-2} yr^{-1}C) measured from brown seaweeds found in natural environments and laboratory experiments.

Specie	Location	Productivity (g m^{-2} yr^{-1}C)	References
Ascophyllum nodosum	(Massachussets,USA)	1179	Roman et al.,1990
A. nodosum	(Nova Scotia, Canada)	959	Cousens (1984)
Ecklonia cava	(Izu Peninsula, Japan)	1044	Yokohama et al., 1987
E. radiata	(Sydney, Australia)	1116	Larkum (1986)
E. radiata	(Goat Island, New Zealand)	2160	Novaczek (1984)

Laminaria joponica	(Qingdao, China)	2200	Chaoyuan et al., (1984)
L. longicruris	(Connecticut,USA)	3400	Egan and Yarish (1990)
L. longicruris	(Nova Scotia, Canada)	2000	Mann (1972)
Macrocystis integrifolia	(British Columbia, Canada)	1300	Wheeler and Druehl (1986)
Sargassum horneri	(Matsushima, Japan)	1496	Taniguchi and Yamada (1988);

Table taken from Gao and McKinley, 1994.

Table S3- Benthic *Sargassum* biomass estimated in this study and the literature. Sites in different cities and states with corresponding Longitude, Latitude, Country/Region, Biomass, and reference are presented.

Longitude	Latitude	Country/Region	Biomass $(g.m^{-2})$	References
-41.6382	-2.88189	Brazil/Piauí (PI)	0.07	This study
-41.6382	-2.88189		0.23	This study
-41.6382	-2.88189		0.98	This study
-41.6382	-2.88189		0.51	This study
-41.6382	-2.88189		0.01	This study
-41.6382	-2.88189		3.01	This study
-41.6382	-2.88189		55.20	This study
-41.6382	-2.88189		268.48	This study
-41.6382	-2.88189		84.48	This study
-41.6382	-2.88189		118.88	This study
-41.6382	-2.88189		0.01	This study
-41.6382	-2.88189		140.16	This study
-41.6382	-2.88189		293.92	This study
-41.6382	-2.88189		0.21	This study
-41.6382	-2.88189		0.11	This study
-41.6382	-2.88189		54.88	This study
-41.6382	-2.88189		99.36	This study
-41.6382	-2.88189		0.04	This study

-41.6382	-2.88189		4.26	This study
-41.6382	-2.88189		0.44	This study
-41.6382	-2.88189		0.74	This study
-41.6382	-2.88189		0.23	This study
-37.4044	-4.6752	Brazil/Ceará (CE)	0.14	This study
-37.4044	-4.6752		0.14	This study
-37.4044	-4.6752		0.14	This study
-37.4044	-4.6752		0.15	This study
-37.4044	-4.6752		0.14	This study
-37.4044	-4.6752		0.14	This study
-37.4044	-4.6752		0.16	This study
-37.4044	-4.6752		0.23	This study
-37.4044	-4.6752		0.23	This study
-37.4044	-4.6752		0.34	This study
-37.4044	-4.6752		0.45	This study
-37.4044	-4.6752		0.52	This study
-37.4044	-4.6752		0.14	This study
-35.0444	-6.2259	Brazil/Rio Grande	89.00	This study
-35.0444	-6.2259	do Norte (RN)	36.15	This study
-35.0444	-6.2259		19.20	This study
-35.0444	-6.2259		250.00	This study
-35.0444	-6.2259		89.00	This study
-35.0444	-6.2259		89.10	This study
-35.0444	-6.2259		100.20	This study
-35.0444	-6.2259		88.00	This study
-35.0444	-6.2259		36.16	This study
-35.0444	-6.2259		39.20	This study
-35.0444	-6.2259		127.20	This study
-35.0444	-6.2259		305.44	This study
-35.0444	-6.2259		18.40	This study
-34.8016	-7.2736	Brazil/Paraíba (PB)	3.32	This study
-34.8016	-7.2736		4.50	This study
-34.8016	-7.2736		2.78	This study
-34.8016	-7.2736		3.56	This study
-34.8016	-7.2736		4.30	This study
-34.8016	-7.2736		4.04	This study
-34.8016	-7.2736		8.90	This study
-34.8016	-7.2736		3.50	This study
-34.8016	-7.2736		2.72	This study
-34.8016	-7.2736		2.34	This study
-36.2952	-10.3564	Brazil/Alagoas (AL)	9.12	This study
-36.2952	-10.3564		0.48	This study
-36.2952	-10.3564		0.49	This study
-36.2952	-10.3564		5.84	This study

-36.2952	-10.3564		9.60	This study
-36.2952	-10.3564		3.25	This study
-36.2952	-10.3564		14.88	This study
-36.2952	-10.3564		5.99	This study
-36.2952	-10.3564		9.50	This study
-36.2952	-10.3564		0.54	This study
-36.2952	-10.3564		1.34	This study
-36.2952	-10.3564		6.70	This study
-36.2952	-10.3564		3.67	This study
-38.3408	-12.9489	Brazil/Bahia (BA)	226.77	This study
-38.3408	-12.9489		213.40	This study
-38.3408	-12.9489		48.98	This study
-38.3408	-12.9489		1.11	This study
-38.3408	-12.9489		295.20	This study
-38.3408	-12.9489		277.94	This study
-38.3408	-12.9489		151.91	This study
-38.3408	-12.9489		4.50	This study
-38.3408	-12.9489		75.34	This study
-38.3408	-12.9489		358.94	This study
-38.3408	-12.9489		74.05	This study
-38.3408	-12.9489		28.25	This study
-38.3408	-12.9489		356.16	This study
-38.3408	-12.9489		248.00	This study
-38.3408	-12.9489		192.64	This study
-38.3408	-12.9489		411.07	This study
-38.3408	-12.9489		109.78	This study
-38.3408	-12.9489		109.91	This study
-38.3408	-12.9489		109.69	This study
-38.3408	-12.9489		267.24	This study
-38.3408	-12.9489		144.49	This study
-38.3408	-12.9489		375.91	This study
-38.3408	-12.9489		294.67	This study
-38.3408	-12.9489		172.18	This study
-38.3408	-12.9489		227.33	This study
-38.3408	-12.9489		304.85	This study
-38.3408	-12.9489		265.43	This study
-38.3408	-12.9489		131.27	This study
-38.3408	-12.9489		193.10	This study
-38.3408	-12.9489		166.64	This study
-40.1591	-20.0319	Brazil/Espírito Santo (ES)	1.61	This study
-40.1591	-20.0319		199.68	This study
-40.1591	-20.0319		64.32	This study
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-40.1591	-20.0319		31.20	This study

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-40.1591	-20.0319		0.74	This study
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-40.1591	-20.0319		258.56	This study
-40.1591	-20.0319		497.60	This study
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-40.1591	-20.0319		325.68	This study
-41.9056	-22.7569	Brazil/Rio de Janeiro (RJ)	3.03	This study
-41.9056	-22.7569		5.16	This study
-41.9056	-22.7569		0.51	This study
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-48.5073	-27.7442		6.16	This study
-48.5073	-27.7442		2.78	This study
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-48.5073	-27.7442		37.12	This study
-48.5073	-27.7442		20.80	This study
-48.5073	-27.7442		42.40	This study
-48.5073	-27.7442		3.70	This study
-74.1905	11.29342	Colombia/Santa Marta	186.55	(Camacho et al., 2012)
-74.1905	11.29342		40.50	(Camacho et al., 2012)
-114.435	29.90946	Mexico/Gulf	1800.00	(Pacheco-Ruíz et al., 2009)
-114.37	29.76959	and Baixa California	1200.00	(Pacheco-Ruíz et al., 2009)
-113.567	29.09509		1780.00	(Pacheco-Ruíz et al., 2009)
-113.567	29.09509		870.00	(Pacheco-Ruíz et al., 2009)
-112.901	28.47355		1980.00	(Pacheco-Ruíz et al., 2009)

-112.755	27.95639		550.00	(Cruz-Ayala et al., 1998)
-112.644	27.71167		460.00	(Cruz-Ayala et al., 1998)
-157.896	21.59827	EUA/Hawai	9.24	(Santellices, 1977)
-158.179	21.40471		0.88	(Russo, 1990)
-69.0002	12.1431	Curaçao	440.00	(Wanders, 1976)
-69.1545	12.36973		4.10	(Engelen et al., 2005)
-68.8527	12.17429		3.90	(Engelen et al., 2005)
119.9088	16.40612	Phillipines	100.00	(Trono and Tolentino, 1993)
119.9088	16.40612		103.00	(Trono and Tolentino, 1993)
120.4667	18.03333		150.00	(Ragaza and Hurtado, 2004)
101.8505	2.411906	Malaysia	47.88	(Wong and Phang, 2004)
101.8505	2.411906		46.00	(Wong and Phang, 2004)
30.97967	-29.9681	Africa	150.00	(Gillespie and Critchley, 2011)
30.97967	-29.9681		80.00	(Gillespie and Critchley, 2011)
30.97967	-29.9681		60.00	(Gillespie and Critchley, 2011)
115.65	-32.2333	Australia	720.00	(Hoang et al., 2016)
146.8624	-19.1534		500.00	(Vuki and Price, 1994)
113.9839	-21.8875		2200.00	(Fulton et al., 2014)

Table S4- Floating *Sargassum* biomass estimated in this study and the literature. Sites in different cities and states with corresponding Longitude, Latitude, Biomass and references are presented.

Longitude	Latitude	Biomass $(g.m^{-2})$	References
-32.4087	-3.85689	98000	(Sissini et al., 2017)
-32.4087	-3.85689	14000	This study
-32.4087	-3.85689	18000	This study
-32.4087	-3.85689	13189	This study
-41.6402	1.95334	3333	(Wang et al., 2019)
-75.9938	33.26079	1.238	(Stoner et al., 1983; Stoner and Greening, 1984)
-68.938	31.81934	0.112	(Stoner et al., 1983; Stoner and Greening, 1984)
-76.3371	32.21727	0.062	(Stoner et al., 1983; Stoner and Greening, 1984)
-63.5305	34.38981	0.08	(Stoner et al., 1983; Stoner and Greening, 1984)
-73.8567	33.38881	0.028	(Stoner et al., 1983; Stoner and Greening, 1984)
-76.6471	23.96446	0.587	(Stoner et al., 1983; Stoner and Greening, 1984)
-76.6471	23.96446	0.165	(Stoner et al., 1983; Stoner and Greening, 1984)
-89.8871	25.06299	0.258	(Stoner et al., 1983; Stoner and Greening, 1984)
-80.0518	26.48743	0.21	(Stoner et al., 1983; Stoner and Greening, 1984)
-80.0518	26.48743	0.28	(Stoner et al., 1983; Stoner and Greening, 1984)
-82.3763	23.38465	0.047	(Stoner et al., 1983; Stoner and Greening, 1984)
-74.9959	14.20087	0.028	(Stoner et al., 1983; Stoner and Greening, 1984)
-89.3564	21.54808	0.013	(Stoner et al., 1983; Stoner and Greening, 1984)
-89.3564	21.54808	0.14	(Stoner et al., 1983; Stoner and Greening, 1984)
-73.4157	40.36319	0.0034	(Stoner et al., 1983; Stoner and Greening, 1984)
-73.4157	40.36319	0.008	(Stoner et al., 1983; Stoner and Greening, 1984)
-75.8638	32.50525	1.067	(Parr, 1939)
-77.9654	32.40233	1.642	(Parr, 1939)
-77.9654	32.40233	0.524	(Parr, 1939)
-76.3388	27.41392	0.00025	(Schell et al., 2015; Howard and Menzies,1969)
-76.3388	27.41392	0.00023	(Schell et al., 2015; Howard and Menzies,1969)
-76.3388	27.41392	0.00017	(Schell et al., 2015; Howard and Menzies,1969)
-59.253	12.24661	0.00084	(Schell et al., 2015; Howard and Menzies,1969)
-59.253	12.24661	0.00007	(Schell et al., 2015; Howard and Menzies,1969)
-79.5551	31.83885	0.24	(Howard and Menzies, 1969)
-79.5551	31.83885	0.2	(Butler et al., 1973; Butler and Stoner,1984)
-76.3371	32.21727	0.219	(Butler et al., 1973; Butler and Stoner,1984)

*References added:

Stoner, 1983; Schell et al., 2015; Butler et al., 1973.

Table S5- The % Carbon estimated in this study and the literature, in floating and benthic *Sargassum* biomass. Continent, Sites, Species, % Carbon and References are presented.

Continent	Sites	Species	% Carbon	References
South America	Piauí (PI)	Benthic	35.66	This study
		Benthic	35.73	
		Benthic	35.73	
	Rio Grande do Norte (RN)	Benthic	32.36	This study
		Benthic	33.20	
		Benthic	33.33	
	Pernambuco (PE)	Benthic	37.29	This study
		Benthic	37.58	
		Benthic	37.29	
		Benthic	37.44	
		Floating	39.02	
		Floating	35.11	
		Floating	42.07	
	Bahia (BA)	Benthic	30.88	This study
		Benthic	37.27	
		Benthic	37.09	
	Espírito Santo (ES)	Benthic	34.47	This study
		Benthic	35.77	
		Benthic	35.13	
	Rio de Janeiro (RJ)	Benthic	36.16	This study
		Benthic	35.77	
		Benthic	44.26	
	São Paulo (SP)	Benthic	35.61	This study
		Benthic	35.69	
		Benthic	34.15	
	Santa Catarina (SC)	Benthic	35.11	This study
		Benthic	36.23	
		Benthic	36.13	
Central America	Woods	Benthic	21.80	(Lapointe, 1995)
	Florida	Benthic	26.00	
	Jamaica	Benthic	11.90	
	Bahamas	Benthic	22.60	
North America	US	Floating	18.70	(Sembera et al., 2018)
	Hawaii	Benthic	30.00	(Atkinson and Smith,1983)
	Hawaii	Benthic	21.00	(Atkinson and Smith,1983)

	Gulf	Floating	26.30		(Hanson, 1977)
	Gulf	Floating	27.10		(Hanson, 1977)
	Gulf	Floating	26.80		(Hanson, 1977)
	Gulf	Floating	27.50		(Hanson, 1977)
	Gulf	Floating	26.40		(Hanson, 1977)
	Gulf	Floating	26.90		(Hanson, 1977)
	Gulf	Floating	25.70		(Hanson, 1977)
	Gulf	Floating	28.60		(Hanson, 1977)
	Gulf	Floating	28.70		(Hanson, 1977)
	Gulf	Floating	26.80		(Hanson, 1977)
Africa	Ondo State	Floating	57.30		(Oyesiku and Egunyomi,2014)
Asia	Singapore west	Benthic		25.68	(Chen and Yang, 2005)
Oceania	N.Queensland	Benthic		30.00	(Hanson, 1977)
	N.Queensland	Benthic		32.00	(Hanson, 1977)
	N.Queensland	Benthic		32.00	(Hanson, 1977)
	W Australia	Benthic		42.00	(Hanson, 1977)

Table S6- Environmental predictors used to model the potential distribution and biomass of *Sargassum*. Predictors were retrieved from Bio-ORACLE 2. Benthic layers were used for benthic *Sargassum* and surface layers for floating *Sargassum*.

Benthic *Sargassum*	Floating *Sargassum*
Environmental predictors	
Minimum Dissolved iron = "Iron"	Minimum Dissolved iron = "Iron"
Minimum Phosphate = "Phosphate"	Minimum Phosphate = "Phosphate"
Minimum Nitrate at = "Nitrate"	Minimum Nitrate at long term= "Nitrate"
Minimum Temperature = "Temp.Min"	Minimum Temperature = "Temp.Min"
Maximum Temperature = "Temp.Max"	Maximum Temperature = "Temp.Max"
Mean Available light at bottom= "Light"	Minimum Photosynthetically Available Radiation= "PAR"
Minimum Salinity= "Salinity"	Minimum Salinity= "Salinity"
	Maximum Sea ice thickness= "Ice"

2.9 References

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CAPÍTULO 2

PHYSIOLOGICAL RESPONSE OF *Sargassum* FORESTS TO GLOBAL WARMING

(O artigo está nas normas do periódico *New Phytologist,* para o qual foi submetido)

CAPÍTULO 2

Physiological response of *Sargassum* forests to global warming

Lidiane P. Gouvêa[a*], Jorge Assis[b], Carlos F. D. Gurgel[a], Eduardo Bastos[a], Ester A. Serrão[b], Leticia M. C. Peres[a], Fernanda Ramlov[c], Gabrielle Koerich[a], Paulo A. Horta[a].

Affiliations:

[a] Phycology Laboratory, Department of Botany, Biological Sciences Center, Federal University of Santa Catarina, Florianopolis, Santa Catarina, Brazil

[b] CCMAR - Centre of Marine Sciences, University of Algarve, Faro, Portugal

[c] Department of Fitotechnique, Center of Agricultural Sciences, Federal University of Santa Catarina, Florianopolis, Santa Catarina, Brazil

*Corresponding author: lidi_pel@hotmail.com

ABSTRACT

Global warming is shifting the distribution of marine species worldwide. The abundant-center hypothesis predicts higher populational abundance in the center of a species' distribution due to more favorable conditions. Accordingly, studies have assumed that all individuals from the same species respond equally to environmental conditions, yet species can perform metabolic/structural changes to adjust physiological performances in response to temperature variations, and multiple lines of evidence show populations exhibiting divergent genetic and phenotypic plasticity. Despite the biogeographic and evolutionary role of thermal plasticity and local adaptation, such key traits have been underrepresented in marine studies. *Sargassum* forests represent a great model to test thermal tolerance plasticity between centre-edge populations, particularly in the Southwestern Atlantic Ocean, where they exhibit a sharp decrease in biomass towards the distributional range limit along Brazilian coastlines. Here, we evaluated the differences in *Sargassum cymosum* ecophysiological adjustment (photosynthetic pigments, secondary metabolites, total sugar, protein, and CN) across a latitudinal gradient, and tested for differences in the thermal tolerance between centre-edge populations. Our results show that ecophysiological adjustments of *Sargassum* are driven by macroecological environmental conditions, which coincide with biogeographical provinces and ecoregions. *Sargassum cymosum* centre-edge populations display contrasting temperature tolerances, but both lose biomass in response to thermal stress. Growth rates were reduced by ~30% when exposed to +3 and +2°C above the control treatments. Edge populations in the warm temperate region will likely be more susceptible under temperatures of 30°C, as growth rates presented negative values. These responses might produce considerable range shifts in the future (year 2100) if populations are exposed to climate conditions above the RCP 6.0 scenarios.

Keywords: *Sargassum cymosum;* climate changes; global warming*;* physiological performances.

3.1 Introduction

Environmental conditions largely shape the spatial/temporal occurrence, growth, reproduction, and survival of marine species (Diaz-Pulido et al., 2012; Harley et al., 2012). Accordingly, the abundant-center hypothesis (Brown, 1984; Safriel, Volis, & Kark, 1994) predicts higher populational abundance in the center of a species' geographic due to the prevalence of more favorable conditions (Brussard, 1984; Whittaker, 1956), while from the center towards the edges, abundance is expected to decrease owing to less suitable conditions and increased interspecific competition (Aitken et al., 2008; Case and Taper, 2000). The main environmental drivers responsible for structuring canopy-forming macroalgal assemblages are light, nutrients, and temperature conditions (Hanelt and Figueroa, 2012; Martínez et al., 2012; Gordillo, 2002). In particular, temperature regulates macroalgal growth (Lobban and Harrison, 1994) by forcing biochemical and physiological adjustments in metabolic pathways to optimize cellular performance under different conditions (Ferreira et al., 2014). When organisms are exposed to extreme conditions above or below physiological tolerances, photosynthesis, resource utilization and growth can severely affect (Hanisak and Harlin, 1978; Wernberg et al., 2016).

Changes in carbon, nitrogen, proteins, and storage carbohydrate content can be used as indicators of seaweed physiological status (Burle et al., 2019; Gouvêa et al., 2017). Differences in chemical composition can be related to CN sources depending on the metabolic demand (Lerdau and Coley, 2002; Rosenberg and Ramus,1982; Polo et al., 2015). Thermal stress affects membrane-associated processes (e.g. stability, biochemical composition), and the efficiency of systems with antioxidant properties such as some secondary metabolites (Bischof and Rautenberger 2012). These metabolites (e.g., phenolic compounds, carotenoids) are associated with protective strategies against environmental stressors (Borowitzka et al., 2016; Mannino and Micheli, 2020; Hargrave et al., 2016; Collen et al., 2007). Overall, cellular mechanisms are expected to manifest different outcomes when populations from contrasting ranges (e.g., center vs. rear edges) are compared (Harley et al., 2012) so that organisms from the same species occurring under different conditions might

investment differently in reproduction, growth, and chemical defense (Kurr and Davies, 2018).

Global warming emphasizes the importance of foundation species in ameliorating or buffering the physical stress of associated biodiversity (Bulleri et al., 2018; Burdett et al., 2019; Halpern et al., 2007). Statistical approaches such as species distribution modelling anticipating the potential effect of future climate conditions on marine biodiversity (e.g., Assis et al., 2016) generally assume that all individuals from the same species display similar physiological responses to environmental changes. However, distinct populations can display different genetic and phenotypic plasticity traits (e.g., Bennet et al., 2015; Ferreira et al., 2015). In comparison to terrestrial systems, the implications of thermal plasticity and adaptation have been underrepresented in marine environment (King et al., 2017).

Throughout the current and past centuries, global climate change has increased ocean temperatures through extreme marine heatwave events (MHWs). These have been particularly aggressive in the northwest Atlantic in 2012 (Mills et al., 2013), the Mediterranean Sea (Darmaraki et al., 2019), the northeast Pacific Ocean from 2013 to 2016 (Di Lorenzo and Mantua, 2016) and the Tasman Sea and tropical Australia from 2015 to 2016 (Oliver et al., 2018; Benthuysen et al., 2018). The global frequency and duration of such temperature anomalies have increased by 34% and 17% along the world's coastlines, respectively, including the Brazilian Atlantic coast (Oliver et al., 2018). Additional changes are anticipated in the Representative concentration pathways (RCPs) scenarios under contrasting greenhouse gas emission projections (IPCC, 2014). Originally, RCP comprise four main projections, ranging from RCP 2.6, representing a high mitigation scenario whereby atmospheric temperatures increase 2 °C above pre-industrial levels by 2100, to RCP 8.5, a scenario potentially raising temperatures up to 4.9 °C (IPCC, 2014). Climate impacts on marine biodiversity can be significantly reduced by limiting warming conditions. In this way, the Paris Agreement initiative demands adaptation and mitigation tools to ease changes up to the RCP 2.6, reducing climate change impacts and increasing the resilience of ecosystem services (McLeod et al., 2011).

Phenotypic traits can change among seaweeds populations to cope with environmental stress, particularly evident along environmental gradients (Vélez et al., 2019). *Sargassum* is canopy-forming macroalgae in tropical and subtropical environments known

for its high biomass, productivity, and carbon stock (Gouvêa et al., 2020). In coastal areas and around offshore islands, it forms dominant communities with vital ecological roles in marine ecosystems. *Sargassum* forests represent a perfect model to address the above topic, particularly in the Southwestern Atlantic intertidal regions, where they follow the abundant-center hypothesis, with a rapid decrease in distribution and biomass near the distributional range limit along Brazilian coastlines. Identifying the nature and magnitude of potential ecological costs of metabolic and structural change is key to understand the impacts of climate change on the distribution and ecological function of marine organisms (Clarke, 2003; Osovitz and Hofmann 2007; Edmunds and Gates 2008).

The main goals of the present study were (1) to assess the differences in *Sargassum cymosum* ecophysiological adjustment (photosynthetic pigments, phenolic compounds, total sugar, protein and CN) across a latitudinal gradient, and (2) test for differences in the thermal tolerance of the species between center and edge populations through laboratory experiment.

3.2 Materials and Methods

3.2.1 Biological sampling across a latitudinal gradient

To test for differences in ecophysiological traits of *Sargassum* across a latitudinal gradient, samples were collected in eight sites (Table S1) covering the warm temperate southwestern Atlantic and tropical southwestern Atlantic regions, as defined by Spalding et al. (2007). Sampling was performed in the two consecutive summers of 2016 and 2017, from January to March. On average, fifteen 0.0625 m^2 quadrats were scraped in each site (120 samples in total). Quadrats were placed randomly along a 20 m transect laid across *Sargassum* beds in the upper subtidal zone during low tides. In the laboratory, epiphytes and epifauna were removed. Species identification followed dichotomous keys and appropriate literature (Nunes et al., 1998; Ouriques, 1997; Pedrini, 2013). Fresh and dry weight were measured using an analytical balance (Marte, AY 220). *Sargassum* samples were dried at 60°C ($\pm$ 2°C) for 48 hours to measure biomass. Fresh samples were stored in -80 ˚C for subsequent chemical analyses.

3.2.2 Environmental data

Environmental data for present-day conditons were accessed from Bio-ORACLE 2 (Assis et al., 2018; Tyberghein et al., 2012), a dataset of marine layers at a spatial resolution of 30 arcmins (~9.2 km at the equator). Benthic variables used in the analyses were temperature, nitrate, phosphate, salinity, and light at bottom (Fig. **1, 2** and **3**; Table 1). Temperature data for the future RCPs 2.6, 4.5, 6.0 and 8.5 scenarios for 2050 and 2100 (see Fig. **5b**) were also accessed from Bio-ORACLE 2.

3.2.3 Temperature experiment

Temperature experiment simulating past heatwave events and future warming scenarios were performed with *Sargassum* samples from two sites with contrasting environmental conditions: Coqueiro (Piauí, Brazil), a center population in tropical conditions (02°53'02" S) and Cardoso (Santa Catarina, Brazil) beaches, an edge population in warm temperate conditions (28°36′31" S). The samples used in the experiment refer to the summer of 2016.

Seawater was sterilized with sand-filters and exposure to ultraviolet light. Samples (1.5 g, n=5) were placed in Erlenmeyer flasks of 250 mL with sterilized seawater and acclimated for 20 days at 28°C (tropical specimens) and 25 ºC (warm temperate specimens) at an irradiance of 400 µmol photons.m^{-2}. s^{-1}. These temperatures were used as the control treatment. Seawater nutrients concentration were analysed for the samples collected at the two sites and were filtered through GF/F Whatman 0.45 µm filters before analysis. Dissolved inorganic nutrients (NO_3^{-2}, NH_4^{+}, PO_4^{-3}) were determined colorimetrically according to Treguer and Le Corre (1975) and Grasshoff et al. (1983), using a spectrophotometer (UV-1100, Pro-Analise ISE Quımica e Diagnostica Ltda, Brazil). Nutrient concentrations obtained seawater of two regions were used in the experiments (see Table S2). The seawater was changed every 48h. The compounds $(NH_4)_2SO_4$, Na_2HPO_4, and $NaNO_3$ were added to seawater to obtain the corresponding concentrations of the environment for each population.

Experimental treatments included the exposure of both populations to four temperatures, 25 ºC, 28 ºC, 30 ºC and 33 ºC, for 30 days. These temperatures were selected based on historical data from the Global Ocean Physics Reanalysis ECMWF, which includes bias correction combining satellite and in situ data (Fig. 4), and also the future RCPs 2.6, 4.5, 6.0 and 8.5 scenarios for 2050 and 2100 (see Fig. 5b).

The relative growth rates (RGR) and Photosynthesis measures were realized in the temperature experiment. The RGR were determined according to Lignell and Pedersén (1989), and following the equation:

Growth rate (GR) = $[(Wt/Wi)^{1/t} - 1] \times 100$

where Wi = initial fresh weight, Wt = final fresh weight, and t = experimental time The results are expressed as a daily percentage [% day^{-1}] of biomass production.

Photosynthetic performance was evaluated *in vivo* (n=4) via Pulse amplitude modulated (PAM) fluorometry of chlorophyll *a* in photosystem II (PSII) using a Jr-PAM (Walz, Germany). The parameters used for the analyses before measuring were gain intensity = 2, measurement light = 8, light pulse = 0.8 s, n = 3 per replica. The maximum quantum yield (Fv/Fm) was determined after acclimation of algae in the dark for 30 minutes. The values were calculated according to the equations from Schreiber et al., (1986).

Photosynthetic O_2 evolution measurements were done using incubations in sealed custom-made acrylic chambers (150 mL) with internal circulation provided by a magnetic stirrer. The samples were incubated with filtered seawater (0.45μm), under the corresponding experimental temperature, for 30 min at 10, 25, 40, 80, 120, 210, 540, 800 and 1200 μmol quanta m^{-2}s^{-1}. The oxygen concentration was measured at the beginning and the end of the incubations with an oximeter (YSI 5000-115, Yellow Springs, USA). Afterwards, the *Sargassum* samples were incubated in darkness for 30 min to determine respiration rates, which allowed for later calculation of gross photosynthesis. The samples were subsequently dried for 48 h at 60 °C, and the calculated dry weight was used to normalize metabolic rates.

3.2.4 Chemical analyses

The following chemical analyzes (pigments, phenolic compounds, total sugar, protein and total organic carbon and nitrogen) were performed for the sampling across latitudinal gradient and temperature experiment.

Photosynthetic pigments

Chlorophylls *a* and *c* concentrations were analyzed from fresh samples previously stored at −80 °C (n = 3). Extracts were prepared from 1.0 g in 5 mL of 90% acetone protected from light. The extracts were centrifuged (EPPENDORF 5810R, Eppendorf AG, Germany) for 5 min at 4000 rpm, and Chlorophyll concentrations were quantified from the supernatants by spectrophotometry at 630, 647, 664, 691 nm (Shimadzu – UV 1800). Calculations followed Ritchie (2008).

Carotenoid extractions were done according to Aman et al. (2005) where 1.0 g of FW (n = 4) was extracted in 10 mL of methanol P.A. Crude extracts were quantified by high-pressure liquid chromatography (HPLC) following Kuhnen et al. (2009), Aliquot samples (10 µL, n = 4) were injected into a liquid chromatographer (Shimadzu LC-10A) equipped with a C18 reverse-phase column (Vydac 218TP54; 250 mm× 4.6 mm, Ø5 µm, 30 °C) and protected by a 5 µm C18 reverse-phase guard column (Vydac 218GK54) and a UV-visible detector (450 nm). Elution was performed with MeOH:CH_3CN (9:1, v/v) at a flow rate of 1 ml min^{-1}. Carotenoid profile identification of fucoxanthin was determined according to retention times of standard compounds. Results are expressed as mg of fucoxanthin per gram of fresh biomass (µg. g^{-1}, DW).

Phenolic Compounds

Phenolic compounds were extracted (1.0 g FW) in 10 mL 80% aqueous (v/v) methanol solution for 1 h, at room temperature and protected from light. Extracts were centrifuged (EPPENDORF 5810R, Eppendorf AG, Germany) for 10 min (4000 rpm), and the supernatant was recovered. Aliquots of 0.3 mL of crude extract were added to 0.225 mL of Folin-Ciocalteu and 2.5 mL of sodium carbonate 20% (w/v) and incubated for 1 h. Absorbance was spectrophotometrically measured at 750 nm (Shimadzu – UV 1800).

Phenolic quantification was based on phloroglucinol acid standard curve ($y = 0.0085x - 0.0036$, R2 = 0.9923).

Total Sugar

The total soluble sugars were separated, according to Shannon (1968). Samples (0.1 g dry weight, n = 5 for each treatment) were extracted with 2 mL of methanol: chloroform: water (MCW; 12: 5: 3) and centrifuged (EPPENDORF 5810R, Eppendorf AG, Germany) at 3000 rpm for 5 min at 25°C. The supernatant and pellet were re-extracted using 2 mL of MCW. The reagents were added one-part chloroform and 1.5-part water to the supernatant, then was centrifuged at 3000 rpm for 5 min, and two phases were obtained. The Anthrone was added 0.2% in the upper aqueous phase (Umbreit & Burris 1957). Afterwards, the measurements of absorbance were obtained spectrophotometrically (Bel Spectro LGS53, BEL Analytical Equipment Ltd., Brazil).

Protein

Soluble proteins were extracted with 0.5 g FW samples (n = 5) in 2 mL of potassium phosphate buffer, according to Bradford (1976). The extracts were centrifuged for 20 min at 750×g, 4°C. Aliquots of 500 μL of supernatant crude extracts were added to 2.5 mL of Bradford reagent. The absorbance of the reaction mixture was measured at 595 nm using a spectrophotometer (Hitachi, Model 100– 20).

Total Organic Carbon and Nitrogen (CN)

Sargassum samples (0.2 g) were lyophilized and acidified to remove inorganic carbon using HCl for 1 min. Samples were neutralized with NaOH for 24 hours and placed them in a desiccator. The total organic matter (TOM) was obtained using High-Temperature Combustion (HTC) at 450 °C for 5 h. Content of organic carbon and nitrogen was estimated using an elemental analyzer. The final dry weight was measured and compared to the initial value. For elemental analysis, each sample was placed in thin tin sheets (Lüdiswiss Sn 98, d 9/10 mm). The analysis was conducted using an Organic Element Analyzer (ECS 4010, Costech Analytical Technologies, Inc., Valencia, California).

3.2.5 Statistical analyses

To analyze the ecophysiological adjustment of distinct *Sargassum* populations, multivariate statistical analyses were performed using hierarchical clustering analysis (HCA), general linear models (GLM) and Distance-based redundancy analysis (db-RDA).

A cluster analysis was performed to the environmental data of Bio-ORACLE 2 (present-day conditions) in order to infer the similarity between sampled sites, by using the Euclidean distance between paired samples (arithmetic mean applied to determine similarities). A Heat map with hierarchical clustering analyses was performed to examine patterns between regions and specimens' chemical compounds.

A generalized linear model (GLM) was fitted using the '*gamma*' distribution and logarithmic link function to evaluate the relationship of maximum temperature (response variable) with chemical compounds and environmental data (explanatory variables). Multicollinearity was addressed by first selecting variables that reduced the variance inflation factor (VIF)(Fox, 2008). Next, a backward model selection procedure was used based on the Akaike information criterion (AIC). Four models were performed, and the best estimated model was inferred with the lowest AIC (Burnham and Anderson, 1998). Model validation was inspected through residuals graphically both for the assumptions of normality and equal variance (Zeileis et al., 2008).

Distance-based redundancy analysis (db-RDA) is a method of multivariate multiple regressions based on any distance measure. It makes a forward selection of the predictor variables, either individually or in specified sets, with tests by permutation (Legendre and Anderson, 1999). In this study, RDA was based on Euclidean distances of biological and environmental data (response variables). The method used a stepwise selection, adjusted R^2 criterion and 4,999 permutations. Because the correlations between our variables were low ($R < 0.5$), no variable was excluded. The data were square-root transformed, and environmental variables were normalized (Clarke and Gorley, 2006). All analyses were performed in R (R Development Core Team, 2016) on RStudio v.3.6.6 (R. Studio Team, 2016).

3.2.6 Temperature experiment

All analyses performed with chemical compounds in the temperature experiment were analyzed by two-way analysis of variance (ANOVA). Newman Keuls Significant Difference post hoc tests were used to identify the statistically different groups. Homogeneity of the variance was tested a priori using Cochran test. All analyses were performed in R (R Development Core Team, 2016) on RStudio v.3.6.6 (R. Studio Team, 2016).

3.3 Results

The environmental variables produced two main clusters along the latitudinal gradient of the Brazilian coastline, which characterizes and reinforce the presence of the tropical and warm temperate biogeographic provinces. The tropical group was further subdivided into two subgroups, while in the warm temperate region only a single group was identified (see Fig. 1). The existence of two tropical subgroups becomes further apparent in heatmap and RDA results (Fig. 2 and 3). When the chemical compounds were compared together with the environmental variables, the same patterns were observed in physiological adjustment of *Sargassum* through the heat map (Fig. 2). Phenolic compounds, biomass, CN, and sugars presented higher concentrations at tropical latitudes, while carotenoids, proteins and chlorophylls were higher in the warm temperate region. These patterns were corroborated by GLM analysis (Table 1). The model showed a negative slope for nitrate, salinity and Chl *a+c,* while for the additional variables, the slope was positive ($p < 0.001$).

RDA analyses showed high power of explanation for the relationships between descriptive and explanatory matrices, with dissolved nutrients directly correlated to the first axis of RDA1, while temperature, light and irradiance inversely correlated to the first axis. Salinity stand out as a major factor explaining the cluster strongly related to the RDA1 (Fig. 3a). The photosynthetic pigments and protein were directly correlated to the first axis of RDA 2, while phenolic compounds, sugar, CN, and biomass were inversely correlated. The first two canonical axes explained 74.90–78.76% of the observed variability, with 59.45 and 68.45% for RDA1 such as 15.45 and 10.31% for RDA 2 (Fig. 3; $R^2 = 0.72$; 0.71). The axis showed the significance of the model through ANOVA (F = 61.03; 95.78; $p < 0.001$).
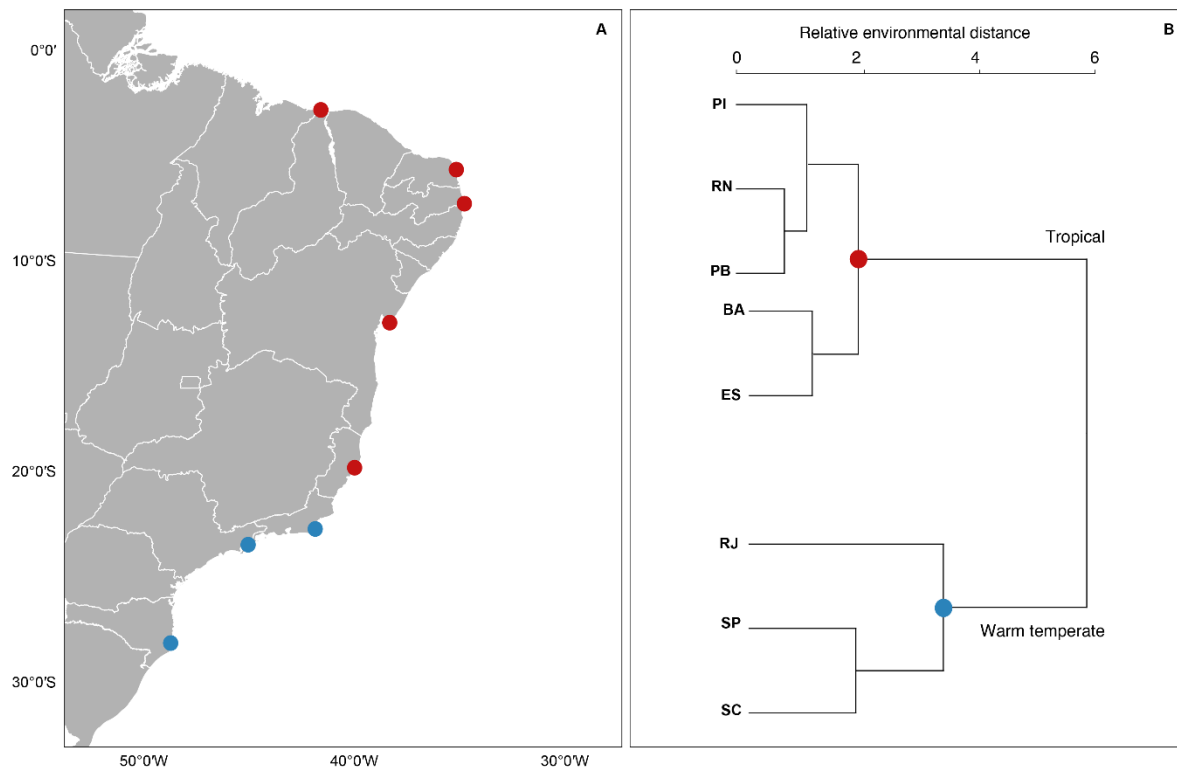
Figure 1: (A) Sites where *Sargassum cymosum* samples were collected along the latitudinal gradient. (B) Cluster analysis of environmental data (maximum temperature, nitrate, phosphate, light at bottom and salinity) separating the sampling sites into two main regions matching the tropical (red circles) and the warm temperate (blue circles) provinces of the Southwestern Atlantic coast, according to Spalding et al. (2007).
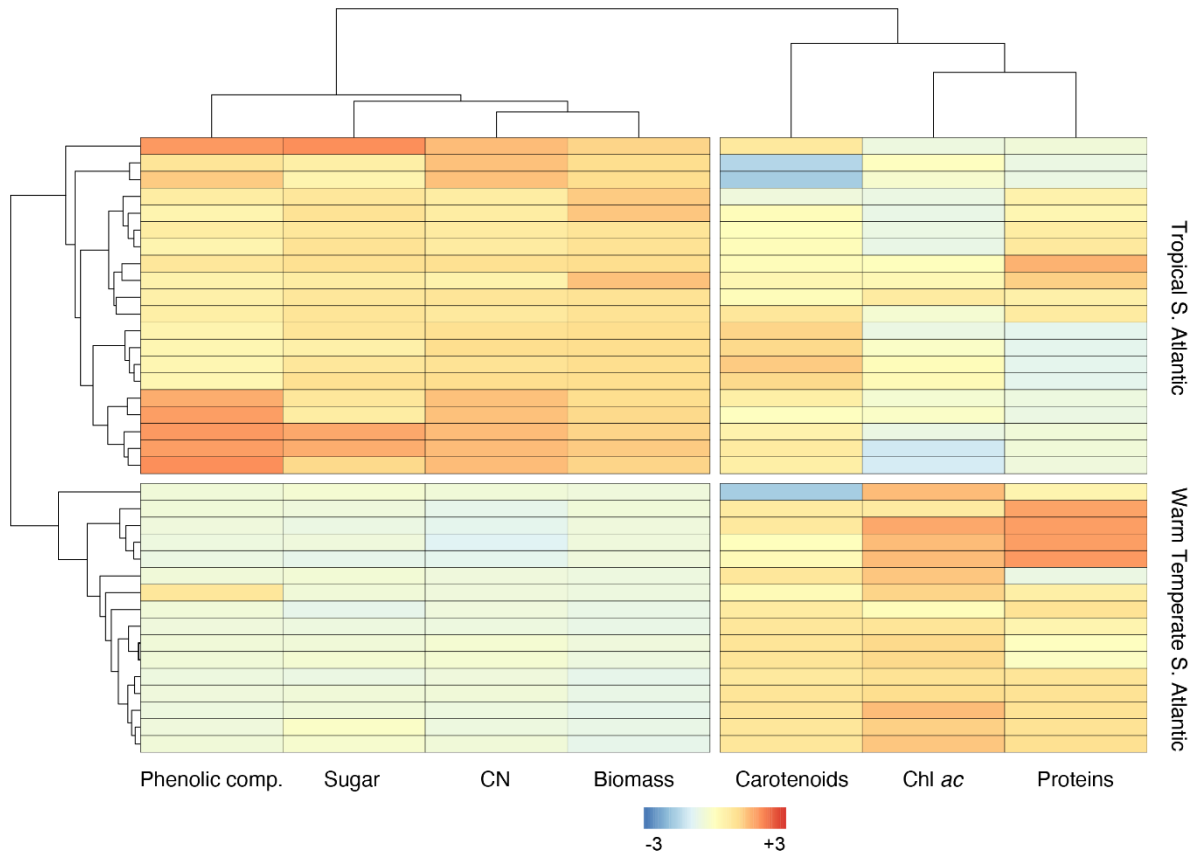
Figure 2: Relationship between environmental clustering and tissue chemical parameters and biomass inferred for 36 *Sargassum cymosum* specimens sampled along the latitudinal gradient. The dendrograms depict hierarchical clustering between regions and samples. The gradient from blue to orange shows values from low to high chemical concentrations / biomass values (-3 and +3 are standardized values).

Table 1: Generalized linear model (GLM; Gamma/log) fitting maximum temperature (response variable) with chemical compounds and environmental data (explanatory variables) with data sampled along a latitudinal gradient. Ten variables were used in the model (Nitrate, Phosphate, Light at bottom, Salinity, CN ratio, Sugar, Protein, Biomass, Chl *a+c*, Phenolic compounds, and Total carotenoids).

Variable	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	5.61	0.02	194.21	< 0.001
Nitrate	-0.013	0.001	-74.52	< 0.001
Phosphate	-0.010	0.001	-71.51	< 0.001
Light at bottom	0.031	0.002	121.07	< 0.001
Salinity	0.069	0.008	85.08	< 0.001
CN ratio	1.07	0.007	144.91	< 0.001
Sugar	0.017	0.006	2.93	< 0.05
Protein	-0.03	0.002	-1.27	0.204
Biomass	4.69	0.001	2.65	< 0.01
Chl a+c	-4.69	0.005	-8.12	< 0.01
Phenolic compounds	-3.85	0.007	-5.14	< 0.001
Total carotenoids	8.64	0.003	3.13	< 0.003
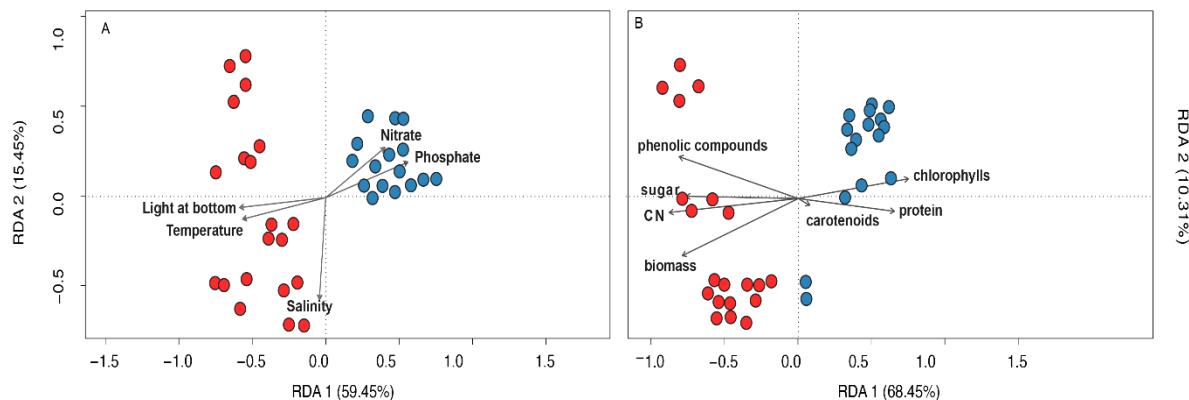
Figure 3: Distance-based redundancy analysis (db-RDA) biplot of first and second axes depicting (A) environmental data and (B) chemical compounds of *Sargassum cymosum* populations in association with tropical (red circles) and warm temperate (blue circles) regions. Axes RDA 1 and RDA 2 showed 59.45–68.45% and 15.45–10.31% of variability distribution, respectively.

3.3.1 Temperature experiment

The temperature experiment showed *Sargassum* populations potentially suffering significant losses in abundance when exposed to extreme warming events (e.g RCP 6.0 and 8.5 by 2100). The responses in relative growth rate (RGR % d^{-1}) agreed with photosynthetic performance (Fig. 5a and S3b). While the present temperatures resulted in maximum RGR for each evaluated population (25°C and 28°C), substantial losses of biomass were observed for specimens from both populations under temperatures that correspond RCP 6.0 and 8.5 by 2100 (from -0.1 to -0.8 % of RGR). The same pattern was observed in productivity and carbon stock (Table S3). Sugar content also varied with increased temperature. The population in the warm temperate region had losses of ~70% at 28°C and 30°C. This had consequences for the CN ratio, which showed ~50% decrease (Fig. S1). In both populations, the increased temperature produced a higher concentration of carotenoids and phenolic compounds (Fig. S2). The population in the tropical region showed chlorophyll concentrations and Fv/Fm with values of 50% lower than those of warm temperate (Fig. S3).
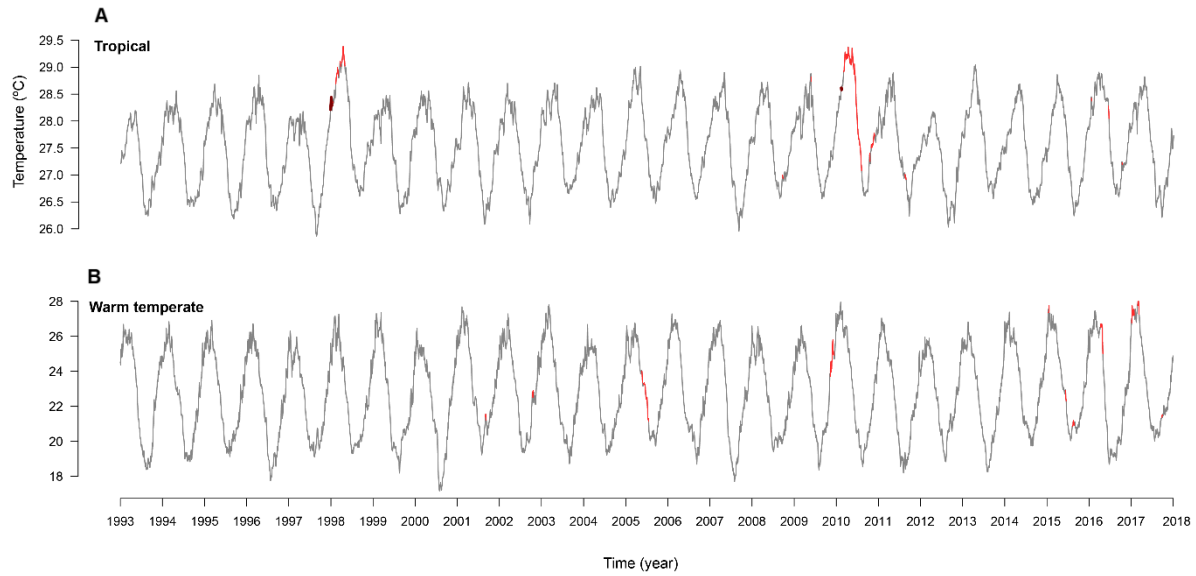
Figure 4: Time series of sea surface temperature (blue) and marine heat wave events (red) for the past 25 years observed in the (A) tropical and (B) warm temperate sites.
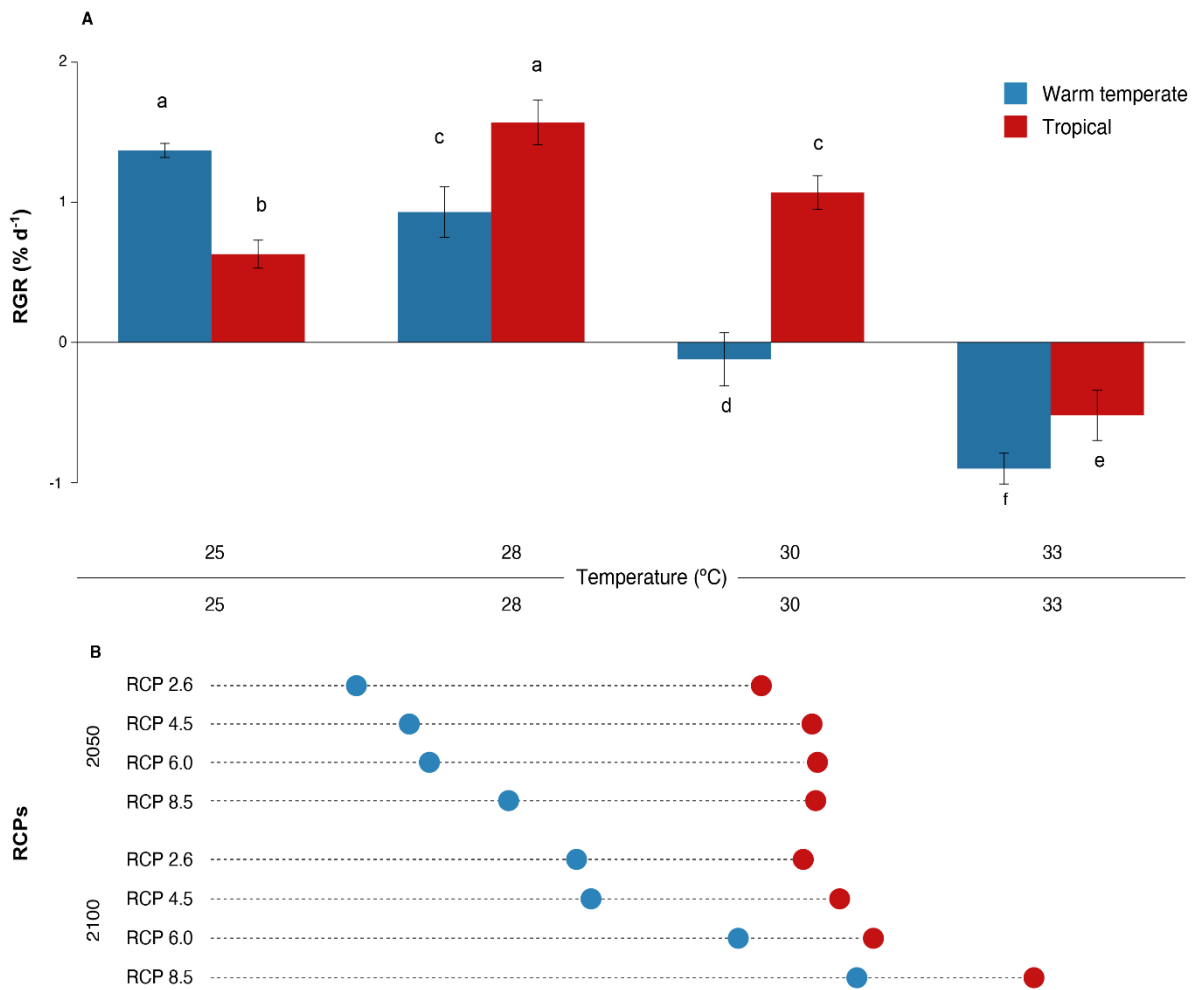
Figure 5: (A) Relative growth rate (RGR% d^{-1}) of warm temperate and tropical *Sargassum* forests under the temperature stress experiment (30 days exposure under 25ºC, 28ºC, 30ºC and 33ºC). Data are shown as mean ±SD (n = 5). Different letters indicate significant differences, p < 0.05 (Newman–Keules test, two-way ANOVA). (B) Temperature projected under contrasting representative concentration pathways (RCPs) for 2050 and 2100.

3.4 Discussion

The present study shows marked ecophysiological adjustments of *Sargassum* forests driven by the macroecological environmental conditions that define their biogeographical provinces and ecoregions (Spalding et al. 2007). These divergences in traits influence hypotheses of consequences of contrasting future outcomes for Brazilian distribution of *Sargassum* (i.e., from center to edge populations), depending on the emission scenario considered. Along a sharp latitudinal gradient, tropical environmental conditions resulted in large biomass and carbon stocks of *Sargassum* forests (CN and sugar, Table 1, Fig. 2 and 3).

This pattern is in line with additional tropical marine ecosystems such as mangroves (Duke et al., 2014) and seagrasses (Short et al., 2007). Ecophysiological adjustments along the gradient further showed increased content of phenolic compounds in the populations of tropical areas. These compounds are known for their antioxidant activity, as well as for photoprotective action and defense against herbivory (Havaux and Niyogi, 1999; Cornish and Garbary, 2010). Previous findings support these results, showing higher concentrations of carotenoids and additional photoprotective compounds in tropical regions (Susanto et al., 2015; Schmitz et al., 2018). Different PAR exposure (i.e., higher towards the tropical areas; Assis et al., 2018) can also induce the production of phenolic compounds in *Sargassum* (Polo et al., 2013). On the other way, increased content of photosynthetic pigments (chlorophylls and carotenoids) was verified in the more temperate areas. Carotenoids act as accessory pigments of photosynthesis and, together with chlorophylls, sustain photosynthetic activity (Balboa et al., 2013, Fig. 2 and 3). The increase of chlorophylls content has been attributed to high nutrient concentration (nitrate and phosphate) in *Sargassum* forests (Gao and Nakahara, 1990), just like the warm temperate conditions and photosynthetic pigments content verified in our study (Fig. 3; Eggert, 2012). Considering RDA analyses, the correlation between nutrients (nitrate and phosphate) and warmer temperate region is known to occur where upwelling contrasts with poor nutrient tropical areas, like in our study region (Pereira et al., 2009). The correlation of tropical conditions and salinity likely results from the higher rate of evaporation by warmer temperatures. Salinity is another important driver affecting the growth and distribution seaweeds (Martins et al., 1999; Wikinson et al., 2007; Assis et al., 2017).

Temperature controls metabolic activities such as photosynthesis and respiration, affecting growth rates and biomass (Davison, 1991). The stress induced by high temperatures produce damages in pigments synthesis, increase of antioxidant compounds, and increases in reactive oxygen species concentration of (ROS) (Balboa et al. 2013). *Sargassum* populations from contrasting regions exhibited different temperature tolerances of up to 3ºC, yet, when exposed to extreme thermal stress, both reduced relative growth rates and lose biomass, particularly evident above temperatures matching the climate scenarios RCP 6.0 and RCP 8.5. Carotenoids act as a protective quencher in high levels of ROS at the cellular level (Zou et al., 2008). This possibly explains the *Sargassum's* strategy of synthesizing carotenoids in exposure to high temperatures as a chemical defensive barrier. These scenarios represent up to +5°C above RCP 2.6 conditions (control treatment), in line with the Paris agreement. In general, the known range of optimal temperature conditions for *Sargassum* species is between 18-30°C (Hanisak and Samuel 1987). In our experiment, temperatures above 28°C and 30°C can produce growth losses of ~30% (Fig. 5), suggesting that *Sargassum* forests might not directly impacted by warming conditions projected by 2050, regardless the RCP scenario. However, by the end of the century, higher emission scenarios (RCP 6.0 and 8.5) might produce harsh conditions for *Sargassum* forests, in previously suitable habitats along the Brazilian coastlines. In Brazil, *Sargassum* is already declining 2.6% per year in the last decades and overall losses sum up to 52% (ranging from 20% to 89%) since systematic records began in 1969 (Gorman et al., 2020). This pattern is paced MHW events (Laurie, 1990), with the potential to strongly genetic diversity levels due to population bottlenecks. For instance, *Sargassum fallax* and *Scytothalia dorycarpa* have loss between 30% to 65% of their average genetic diversity due to population declines while exposed to a heatwave event (Gurgel et al., 2020). Acordingly, the present study allows hypothesizing major negative outcomes for the distribution and genetic diversity levels of *Sargassum cymosum* under emission scenarios above the expectations of the Paris agreement. Physiological adjustment has consequences in net carbon fixation that can result from increased respiration under higher temperatures and/or re-allocation of energy derived from photosynthesis (Huppe and Turpin, 1994). These processes are related to the decrease in productivity and CN of the two populations (Table S3). In the temperature experiment an increase in the concentration of carotenoids was observed potentially due to the oxidative stress suffered by *Sargassum*, as

well as the capacity of the seaweed to dissipate the excess energy (Costa et al., 2017; Torres et al., 2015). Besides that, carotenoids were degraded inversely of chlorophyll content, indicating their role as an energy source for the maintenance of physiological integrity (Fig. S2 and S3).

Under the Paris Climate Agreement, nearly all countries in the world agreed to pursue efforts to limit the increase of temperature to 1.5 °C (UNFCCC, 2015). However, emission reduction goals and carbon budgets for meeting the 1.5 and 2°C climate targets are still unsure. Scenario shows that achieving these objectives requires deep reductions in greenhouse gas emissions. In this way, an essential challenge for climate change research will be to find generalizations about the nature of thermal-safety margins among and within populations to facilitate a better understanding of climate change impacts and identify vulnerable populations. The crucial demand for CO_2 mitigation and the threats of growing coastal urbanization represent arguments to standout *Sargassum* species, as a primary target for conservation, management, and eventual restoration initiatives in a global context.

3.5 Fundings

3.5.1 Declaration of interests

The authors declare no conflict of interest.

.7.1 Declaration of competing interest

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

3.6 Appendix

3.6.1 Supplementary Material (Figures S1-S3)

Physiological response of *Sargassum* forests to global warming

Lidiane P. Gouvêa[a*], Jorge Assis[b], Carlos F. D. Gurgel[a], Eduardo Bastos[a], Ester A. Serrão[b], Leticia M. C. Peres[a], Fernanda Ramlov[c], Gabrielle Koerich[a], Paulo A. Horta[a].

Affiliations:

[a] Phycology Laboratory, Department of Botany, Biological Sciences Center, Federal University of Santa Catarina, Florianopolis, Santa Catarina, Brazil

[b] CCMAR - Centre of Marine Sciences, University of Algarve, Faro, Portugal

[c] Department of Fitotechnique, Center of Agricultural Sciences, Federal University of Santa Catarina, Florianopolis, Santa Catarina, Brazil

*Corresponding author: lidi_pel@hotmail.com

a

b

Figure S1: (a) Sugar and (b) CN ratio present in *S. cymosum* collected in W. temperate and Tropical environment submitted to different temperatures (25ºC, 28ºC, 30ºC and 33 ºC) after 30 days. Data are shown as mean+-SD (n=5). Different letters indicate significant differences (Newman–Keulen test, two-way ANOVA).
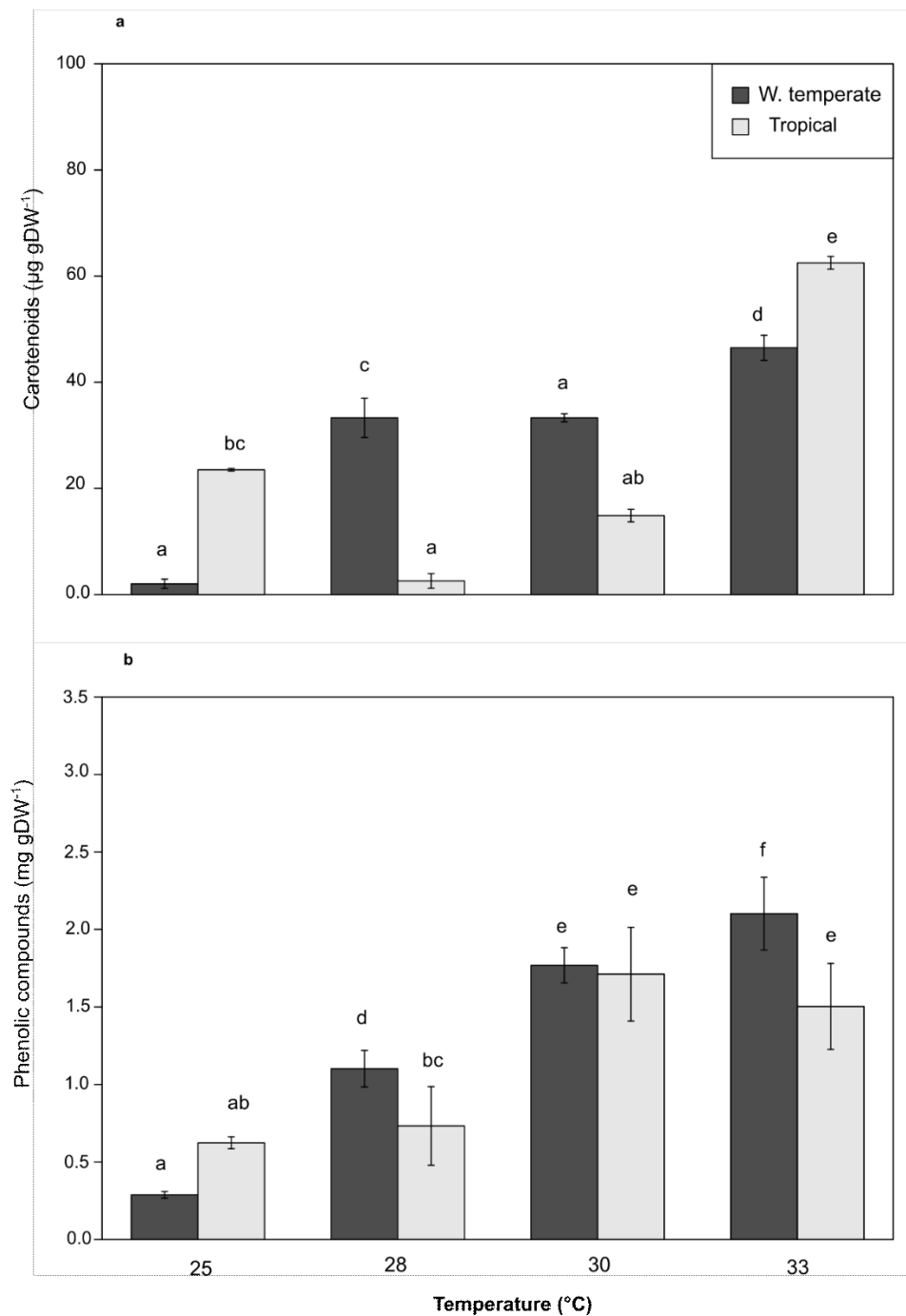
Figure S2: (a) Carotenoids and (b) Phenolic compounds present in *S. cymosum* collected in W. temperate and Tropical environment submitted to different temperatures (25ºC, 28ºC, 30ºC and 33 ºC) after 30 days. Data are shown as mean+-SD (n=5). Different letters indicate significant differences (Newman–Keulen test, two-way ANOVA).
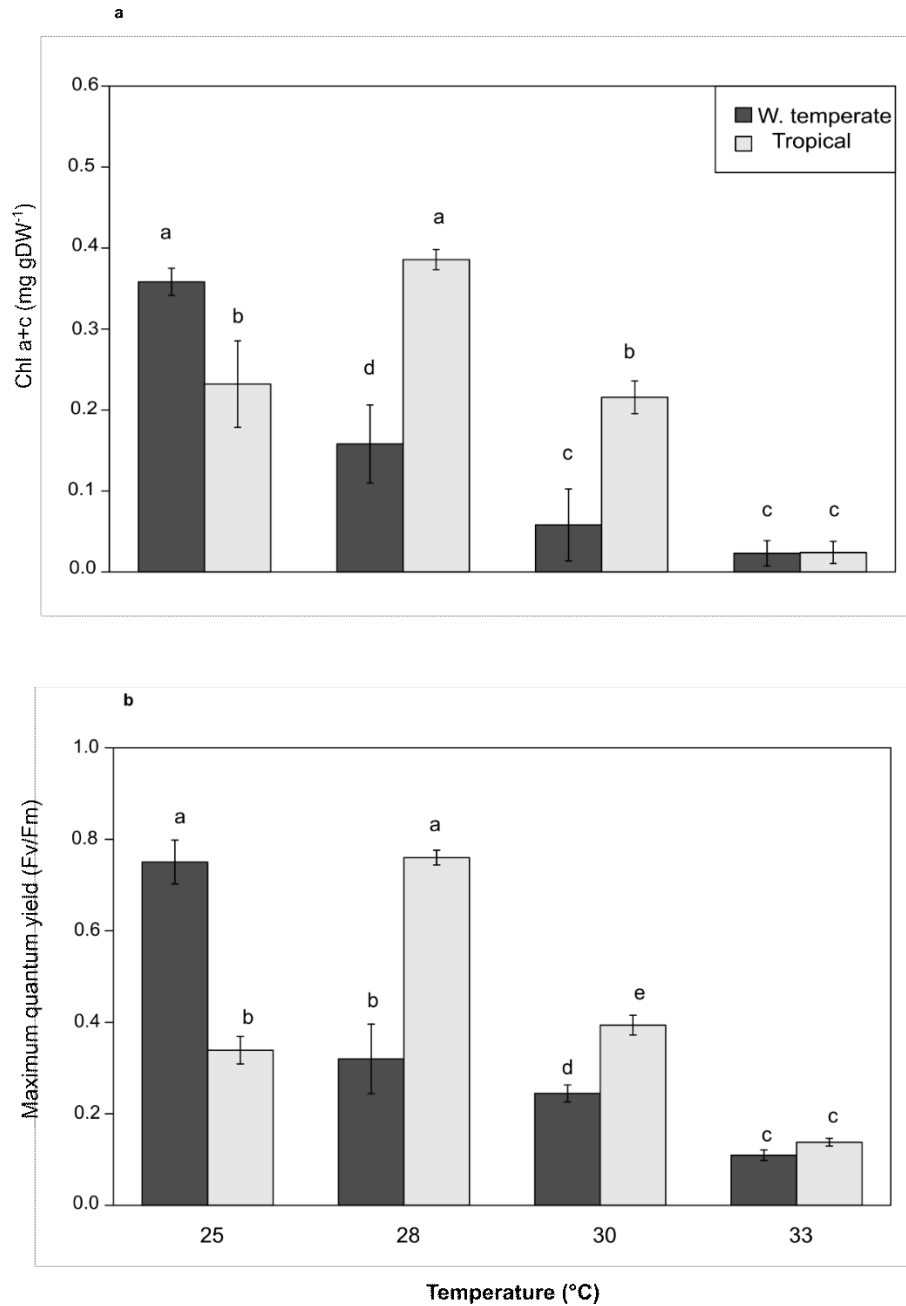
Figure S3: (a) Chl a+c and (b) Maximum quantum yield (Fv/Fm) present in *S. cymosum* collected in W. temperate and Tropical environment submitted to different temperatures (25ºC, 28ºC, 30ºC and 33 ºC) after 30 days. Data are shown as mean+-SD (n=5). Different letters indicate significant differences (Newman–Keules test, two-way ANOVA).

3.6.2 Supplementary Material (Tables S1–S4)

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Affiliations:

[a] Phycology Laboratory, Department of Botany, Biological Sciences Center, Federal University of Santa Catarina, Florianopolis, Santa Catarina, Brazil

[b] CCMAR - Centre of Marine Sciences, University of Algarve, Faro, Portugal

[c] Department of Fitotechnique, Center of Agricultural Sciences, Federal University of Santa Catarina, Florianopolis, Santa Catarina, Brazil

*Corresponding author: lidi_pel@hotmail.com

Table S1: Different sites where *Sargassum cymosum* specimens were collected along the Brazilian coast between February 2016 and March 2017.

Site	City	State	Latitude	Longitude	Substrate
Coqueiro beach	Luís Correia	PI	02°53'02" S	41°38'07"W	Reef
Pipa beach	Tibau do Sul	RN	06°13'23"S	35°02'29"W	Reef
Amor beach	Conde	PB	07°16'25"S	34°48'07"W	Reef
Porto seguro	Arraial D'ajuda	BA	16°29'23" S	39°04'2.6" W	Reef
Cerca beach	Gurarapari	ES	20°39′11.76″S	40°28′20.60″W	Rocky shore
Tartaruga beach	Arm.dos Búzios	RJ	22°45'25"S	41°54'20"W	Rocky shore
Costa beach	Ubatuba	SP	23°26'02"S	45°05'09"W	Rocky shore
Cardoso beach	Laguna	SC	28°36′31"S	48°49′14"W	Rocky shore

Table S2: Environmental variables from two coastal locations in Brazil: a tropical and a warm temperate region. These average values were used as control condition in the experiments.

Region	Variable				
	Ammonium (µM)	Nitrate (µM)	Phosphate (µM)	Salinity (PSS)	Temperature (˚C)
Tropical	1.08	1.52	0.35	36.27	28.70
Warm temperate	1.36	2.67	1.39	36.40	25.74

Table S3: Values of Net primary productivity (NPP; mgC m^{-2} d^{-1}) measure from *Sargassum cymosum* specimens exposed to four different temperatures (25ºC, 28ºC, 30ºC and 33 ºC) after 30 days. Two populations were tested a tropical and a warm region. Different letters indicate significant differences (Newman– Keuls test, two-way ANOVA, p<0.001).

Population	Temperature (°C)	Productivity (mgC m^{-2} d^{-1})
Tropical	25	1.56±0.20^c
	28	3.86±0.35^e
	30	2.91±0.33^d
	33	-0.01±0.02^a
Warm temperate	25	2.13±0.01^d
	28	1.06±0.09^c
	30	-0.02±0.01^a
	33	-0.05±0.01^{ab}

Table S4: Results of two-way ANOVA for different parameters determined in *Sargassum cymosum* samples after exposure for 30 d to different temperatures. Significant effects are indicated in bold.

Variation source	Region			Temperature			Region x Temperature		
	MS	F	*p*	MS	F	*p*	MS	F	*p*
%RGR	0.73	650.22	**0.00**	4.50	400.26	**0.01**	1.02	913.77	**0.00**
Sugar	2.79	35.37	**0.00**	3.26	41.28	**0.01**	6.56	81.10	**0.00**
CN	2.01	24.36	**0.00**	2.12	31.98	**0.00**	4.01	69.87	**0.00**
Carotenoids	0.01	2.44	0.13	0.26	49.47	**0.01**	0.08	16.05	**0.00**
Phenolic compounds	0.56	14.44	**0.00**	3.39	85.85	**0.00**	0.74	18.72	**0.00**
Chlorophylls	0.02	24.50	**0.00**	0.09	92.33	**0.00**	0.03	36.43	**0.00**
Photosynthesis (Fv/Fm)	0.01	15.31	**0.00**	0.43	338.89	**0.00**	0.03	29.61	**0.00**

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CAPÍTULO 3

GLOBAL LOSS OF AREA AND BIOMASS OF THE MANGROVE FOREST BIOME PROJECTED FOR CONTRASTING SCENARIOS OF FUTURE CLIMATE CHANGE

(O artigo está nas normas do periódico *Global Ecology and Biogeography,* para o qual foi submetido)

CAPÍTULO 3

Global loss of area and biomass of the mangrove forest biome projected for contrasting scenarios of future climate change

Lidiane P. Gouvêa[1*], Jorge Assis[2], Kyle Cavanaugh[3], Ester A. Serrão[2], Carlos F.D. Gurgel[1], Paulo A. Horta[1]

Affiliations:

[1] Phycology Laboratory, Department of Botany, Biological Sciences Center, Federal University of Santa Catarina, Florianopolis, Santa Catarina, Brazil

[2] CCMAR - Centre of Marine Sciences, University of Algarve, Faro, Portugal

[3]Department of Geography, University of California, Los Angeles, Los Angeles, California

*Corresponding author: lidi_pel@hotmail.com

ABSTRACT

Over the past 50 years, anthropogenic activities have led to the disappearance of approximately one-third of the world's mangrove forests and their associated ecosystem services. To estimate the potential loss of mangrove forest under scenarios of future climate change, we modelled global distributional and biomass shifts.

Distribution and biomass changes of mangrove forests were predicted with the machine learning algorithm Boosted Regression Trees (BRT). Occurrence and aboveground biomass (AGB) data were gathered globally from GBIF and the available literature. Environmental predictors used in the models were sea and air surface temperatures (long-term series of minima and maxima, °C), Total Cloud fraction and Precipitation (mm yr^{-1}). The data were retrieved from Bio-ORACLE 2 for the present and the RCP 2.6 and 8.5 most contrasting greenhouse gas concentration scenarios for 2100. On the global scale, the models produced for the present estimated a total area of 168,063 Km^2, and a mean and overall biomass of 114.34 t·ha^{-1} and 2.21 Pg, respectively. Both scenarios (RCP 2.6 and RCP 8.5) estimated area losses between 5 and 14.41 %, respectively. In the most drastic scenario, RCP 8.5, almost half of the global biomass might be potentially lost. Pacific islands, South America, and Southeast Asia had projected losses of mangrove area around 16 to 25% in RCP 8.5. The total losses in biomass varied between 26 and 42%. Our estimates can be used to evaluate consequences for lower mangrove carbon sequestration at large scales, to support policy and management. Broad compliance with the Paris Agreement coupled with conservation are important to counteract these projected losses. Our results are also important for planning of restoration actions to include future habitat suitability.

Keywords: Mangrove forests; Climate changes; Aboveground biomass; Distribution and biomass modelling; Boosted Regression Trees; RCP 2.6 and 8.5 scenarios.

4.1 Introduction

The Paris Agreement under the United Nations Sustainable Development Goals demands adaptation and mitigation tools to reduce climate change impacts and increase the resilience of ecosystem services (Damian et al., 2018; McLeod et al., 2011). Coastal and marine systems will be an important focus for mitigation efforts (Gattuso et al., 2018), as they represent an effective carbon sink with the potential to absorb up to 35% of anthropogenic CO_2 emissions (Khatiwala et al., 2009). In this context, coastal wetlands (mangroves, tidal marshes, seagrasses, and seaweeds) are increasingly being recognized as essential carbon sinks (Hiraishi et al., 2014), with mangrove forests alone capturing four times more carbon than rainforests per unit area (Sanderman et al., 2018). Their net primary production (NPP) in AGB can vary between ~11 and 19 Mg C ha^{-1} yr^{-1} (Sherman et al., 2003; Alongi, 2009; Kamruzzaman et al., 2017) and is on the same order of magnitude of terrestrial humid evergreen forests (10.8 Mg C ha^{-1} y^{-1}) and peat swamp forests (11.1 MgC ha^{-1} y^{-1}) (Malhi et al., 2011; Alongi, 2014). Carbon burial accounts ~15% of the total organic carbon in marine environments and this blue carbon is considered significant long-term storage (Mcleod et al., 2011; Bouillon et al., 2003; Alongi, 2014; Breithaupt et al., 2012).

Besides carbon sequestration, mangrove forests provide other key ecosystem services (Donato et al., 2011; Komiyama, 2014) such as protecting coastal areas from erosion and extreme weather events (Doughty et al., 2017) and providing habitat and energy to associated ecological communities (Lavieren et al., 2012). An example is the reduction of damage from tsunami impacts, as areas protected by healthy mangroves suffered ten times less impact than degraded areas (Dahdouh-Guebas, 2006). Altogether, the financial return of all mangrove services is estimated in US$ 194,000/ha/year, with a global value of US$ 2.748 trillion per year (Barbier et al., 2011, Costanza et al., 2014).

Over the past 50 years, anthropogenic activities, in particular deforestation, have led to the disappearance of approximately one-third of the world's mangrove forests (Alongi, 2002) and their associated ecosystem services (Alongi, 2008; DasGupta & Shaw, 2013). The loss of mangroves has led to a decline in global CO_2 uptake and an increase in the emission of greenhouse gases (GHG) from the below-ground biomass by microbial respiration (Howard et al., 2017). Centuries to millennia of accumulated carbon is released in a few decades when

coastal wetlands are drained or otherwise lost. Between 1980 and 2005, it is estimated that 35,000 km^2 of mangrove forest were lost (Spalding, 2010) and this area will continue to emit 0.07 Gt CO_2 over the next few decades. The possible loss of the remaining 152,308 km^2 of mangrove forest might release 0.3 Gt CO_2 over the same time interval (Crooks et al., 2011).

On the other hand, warming has been associated with the expansion of mangroves into salt marsh habitat at higher latitude mangrove range margins (Saintilan et al., 2014, Cavanaugh et al., 2014), which may lead to increased carbon storage in these areas (Kelleway et al., 2017). Climate change has the potential to lead to further losses as large-scale diebacks have been associated with extreme weather events such as severe droughts (Duke et al., 2017; Servino et al., 2018). Extreme weather events may become more frequent and intense in the future and events such as El Niño can decrease rainfall rates and increase evapotranspiration, impacting mangroves (Allen et al., 2015; Brimelow et al., 2017).

Aboveground biomass (AGB) represents a substantial part of the organic carbon reservoir of mangrove forests (Rovai et al., 2016). Mangrove AGB plays a crucial role in the carbon cycle, although with great spatial variability throughout the globe (Donato et al., 2011; Lugo et al., 2014; Rovai et al., 2016) that might be intensified owing to anticipated climate change (Schaeffer-Novelli et al., 2016). Mangrove forests change biomass allocation with physiological responses to thermal conditions (Wang et al., 2017). Moderate warming can produce positive effects on the overall growth of mangroves, particularly in subtropical regions (Akaji et al., 2019), but when temperatures surpass physiological thresholds of photosynthesis, productivity and AGB might be reduced (Clough, 1998). An additional effect of climate change is the alteration of tropical rainfall patterns, which might further impact the growth of mangroves by producing changes in evaporation and transpiration rates. Rainfall is projected to rise up to 25%, yet with substantial regional variation in the magnitude and direction of changes (Houghton et al., 2001). Areas experiencing reductions in rainfall might suffer a conversion of upper tidal zones to hypersaline mudflats, which could reduce biomass, NPP, and lead to mortality of mangrove adults and seedlings (Field, 1995; Ellison, 2000). In contrast, precipitation increases have been associated with mangrove expansions into salt marshes (Eslami-Andargoli et al., 2009).

Carbon stored in coastal ecosystems, such as mangroves has recently been integrated into the international policy agenda through the UNFCCC's Paris Agreement. As a result,

the countries that have mangrove forests within national boundaries will need to track the amount of carbon stored in these systems. Furthermore, there is a need to understand better the impacts of climate change on mangrove spatial distribution and carbon storage, so that national estimates of carbon stocks can be used for decision-making and application of future climate change mitigation approaches. The Intergovernmental Panel on Climate Change highlights the necessity to provide estimations with the lowest possible uncertainty, of changes in carbon stocks and areas (Bolivar et al., 2017). The development of tools such as AGB models at the global scale could help to identify the main mangrove carbon sink areas, including predictive variables that account for significant levels of spatial variability (Ewel et al., 1998; Kristensen et al., 2008). Accurate estimations of mangrove forest biomass continue difficult compared to other forest ecosystems (Pham et al., 2018). Global estimates of AGB in mangroves are limited by the precision of models due to the generalization of allometric equations that are specific to varied tropical and subtropical coastal environments (Wang et al., 2020). However, models to predict the loss of mangrove biomass under climate changes in the future have not yet been developed on a global scale.

In this study, we report changes in mangrove forest AGB and area under contrasting scenarios of future climate change (RCP 2.6 and 8.5) by modelling global distributional and biomass shifts. Our estimates of AGB loss of mangrove forests on a global scale help to assess their contribution to carbon sequestration at larger scales to align with policy requirements. Our model predictions can also guide conservation priorities for mangrove forests, and account for future habitat suitability in restoration planning.

4.2 Methods

Occurrence and AGB data were gathered globally from the Global Biodiversity Information Facility (GBIF, 2020; Spalding & Parret, 2019) and the available literature (Table S1). Six environmental data layers were retrieved from Bio-ORACLE 2 (Tyberghein et al., 2012; Assis et al., 2018) for present-day conditions (from 2000 to 2017) and contrasting representative concentration pathways (RCP; decade 2090–2100) according to the biological relevance for mangrove forest (Hutchison et al., 2014; Numbere & Camilo, 2017; Osland et al., 2017; Wang et al., 2017). Particularly, sea and air surface temperatures (long-term series

of monthly minima and maxima, °C), total cloud fraction and precipitation (mm yr^{-1}) were used in the models. The layers were available at a spatial resolution of 30 arcmins (~9.2 km at the equator).

To predict distribution and biomass changes of mangrove forests the machine learning algorithm Boosted Regression Trees (BRT) was used since it handles non-linear relationships and complex interactions, and systematically retrieves high predictive performances (Elith et al., 2008; Assis et al., 2016). The method used a two-phase approach of (1) fitting models between mangrove occurrence records (i.e., presence and absences) and the environment with a "Bernoulli" distribution, and (2) fitting models between aboveground biomass (AGB) and the environment with a "Gaussian" distribution where the species was firstly predicted to exist (e.g., Barry & Welsh, 2002). Due to the high correlation inferred between marine and air temperature layers (Pearson's R > 0.85; Fig. S1), models were performed separately for the two realms and averaged in a final ensemble.

A cross-validation framework using independent latitudinal bands (e.g., Assis et al., 2016) was implemented to select the optimal BRT parameters reducing overfitting (Elith et al., 2008) and to assess predictive performances (i.e., the potential for model transferability). In this process, different parameter combinations of tree complexity (0.01 to 0.001, step 0.001), number of trees (50 to 1000, step 50) and learning rate (1 to 6) were tested and compared with deviance explained (Elith et al., 2008). To further reduce overfitting, specific forcing of monotonic responses (Assis et al., 2016; Hofner et al., 2011) were forced in the models (positive for minimum temperature, precipitation, and Cloud; negative for maximum temperature) (Elith et al., 2008).

To remove surplus information from the models predicting the occurrence of mangrove forests, records were gridded to the spatial resolution of environmental data layers, and duplicate occurrences were removed. Also, a spatial autocorrelation function was used through the Mantel test to select one record only within the distances estimated as significantly autocorrelated (Fig. S2; Segurado et al., 2006). Due to the lack of absence data, pseudo-absences were randomly generated throughout the whole study areas, in a 1:1 ratio with presence data, except in the localities where mangrove forests occur (Assis et al., 2016; Cerasoli et al., 2017). The final accuracy of occurrence models was described with the area under the receiver operating characteristic curve (AUC) and True skill statistics (TSS). The

performance of biomass models was described with deviance explained. The ecological significance of both models was investigated by determining the contribution of each environmental predictor to the performance of models (Elith et al., 2008). Predicted distributional areas (in km^2) and AGB were estimated for the present and the RCPs per marine ecoregions (Spalding, 2010). In this process, models predicting distributions were reclassified to binomial responses using a threshold allowing to maximize the agreement between observed and predicted presences and pseudo-absences (i.e., maximization of true skill statistics, e.g., Assis et al., 2016). All analyses were performed in R (R Development Core Team, 2019) and RStudio v.3.6.6 (Team, R. 2019). All maps were edited in QGIS (QGIS Development Team, 2019).

4.3 Results

Data compilation from GBIF and literature retrieved 428 and 153 records of occurrence and biomass, respectively (Fig. 1, Table S1). The distribution and biomass models displayed high performance (Threshold 0.20 and TSS 0.90; AUC 0.89) and the little deviation between observations and predictions (Deviance Explained 0.70, see Fig. S2). A combination of physiologically meaningful predictors explained the distribution of species (Fig. S3). Minimum temperature and cloud covers were particularly important for the occurrence of species (relative contributions > 10%; Fig. 2a), while for biomass, data variability was mostly explained by minimum and maximum temperatures, as well as precipitation (relative contributions > 10%; Fig. 2b).

Mangrove forests were predicted to have high suitability in tropical and subtropical environments, corresponding to the known distribution of the biome (Fig. 1). On the global scale, the models produced for the present estimated a total area of 168,063 Km^2, and a mean and overall biomass of 114.34 t·ha^{-1} and 2.21 Pg, respectively (Table 1). Areas and biomasses determined per ecoregion, according to Spalding et al. (2010), are shown in Tables 2 and 3.

Both scenarios (RCP 2.6 and RCP 8.5) projected a decrease in the potential global area of occurrence and biomass (Figs 3 and 4). The total area had losses of 5 and 14.41 %, respectively. The RCP 8.5 scenario indicated that almost half of the global biomass would be lost.

The models predicted that some regions would be more affected than others, with Pacific islands, South America, and Southeast Asia with losses around 16 to 25% of the area in RCP 8.5 (Figs 2 and 3). The losses in total AGB (Tg) varied between 26 and 42%. These values can reach losses of ~51% in Southeast Asia under the worst scenario. This region accounts for almost half of total global AGB and per unit area, currently (792.16 Pg; 196.14 t·ha^{-1}; Table 3). The two regions that showed no losses in AGB and area were the Middle East and South Asia in the RCP 2.6 scenario.

a) Presence and biomass records

b) Distribution model [occurrence]

Probability of occurrence

c) Biomass model
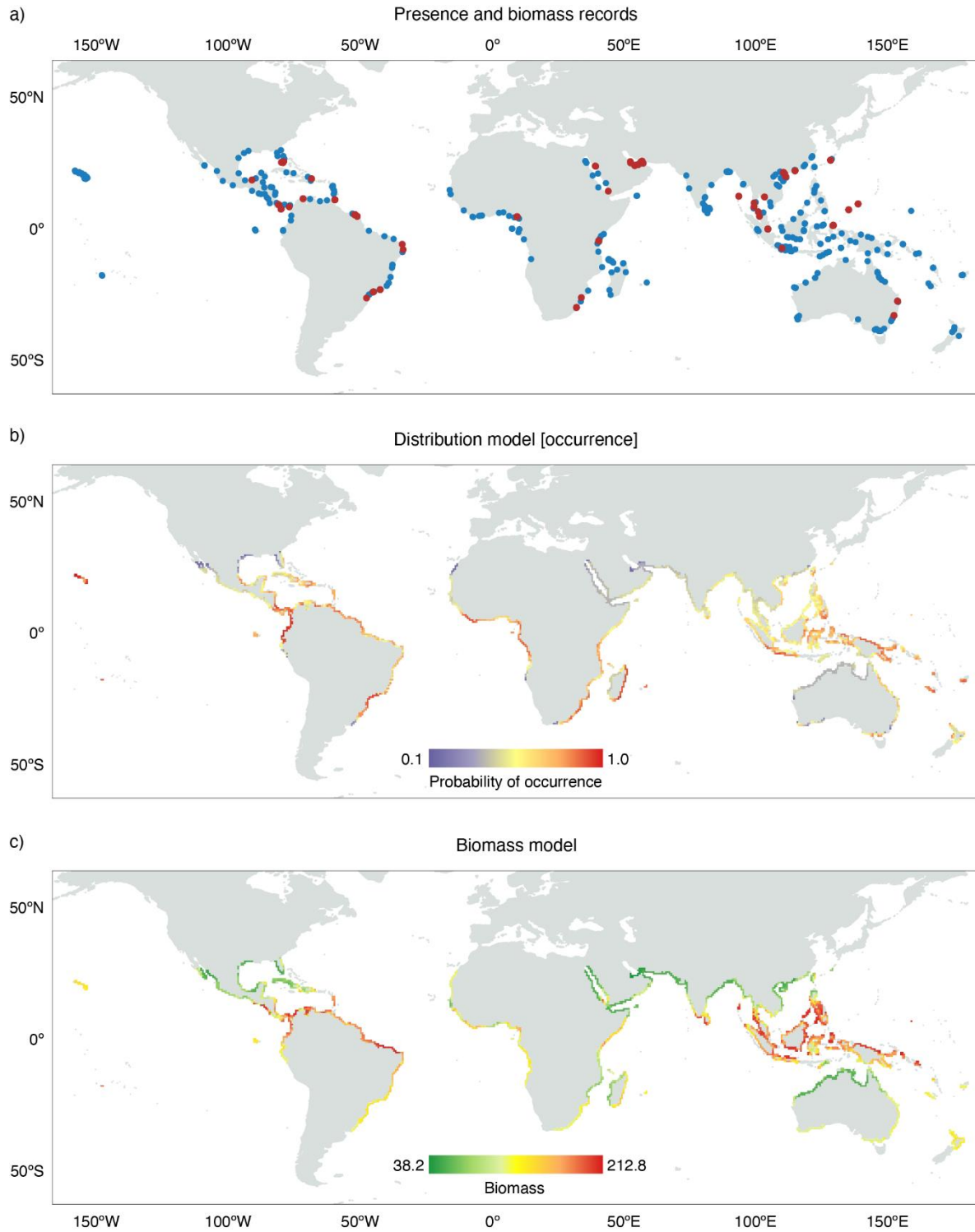
Biomass

Figure 1: (a) Records of occurrence (blue circles) and biomass (red circles) of mangrove forests (biome). (b) Potential global distribution of mangrove forests as the probability of occurrence and (c) predicted biomass (t·ha^{-1}) for the present.

	Distribution model [occurrence]		Biomass model	
Predictor	Relative influence (%)	Threshold	Relative influence (%)	Threshold
a)				
Air min Temp (°C)		8		20
Cloud cover		0.1		0.2
Precipitation (mm yr^{-1})		1000		1000
Air max Temp (°C)		30		28
b)				
Sea min Temp (°C)		10		26
Cloud cover		0.1		0.1
Sea max Temp (°C)		30		30
Precipitation (mm yr^{-1})		1000		1000
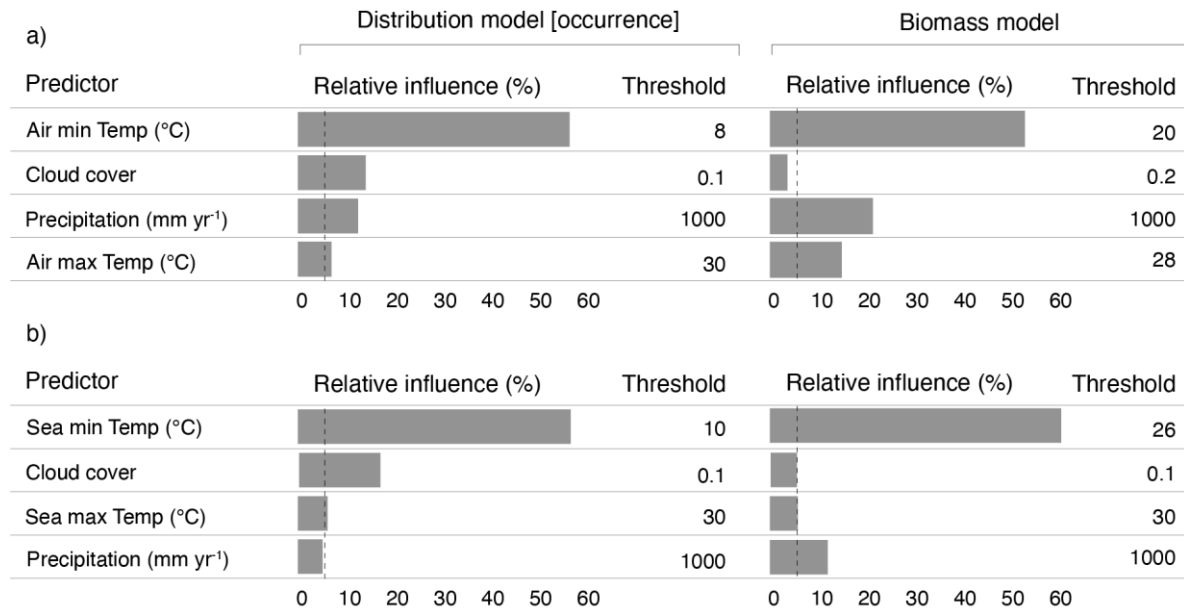
Figure 2: Relative contribution (%) and threshold of the environmental variables used to model the distribution and biomass of mangrove forests with (a) Atmospheric temperatures and (**b**) and Sea temperatures. Dotted lines depict contribution threshold of 5%.
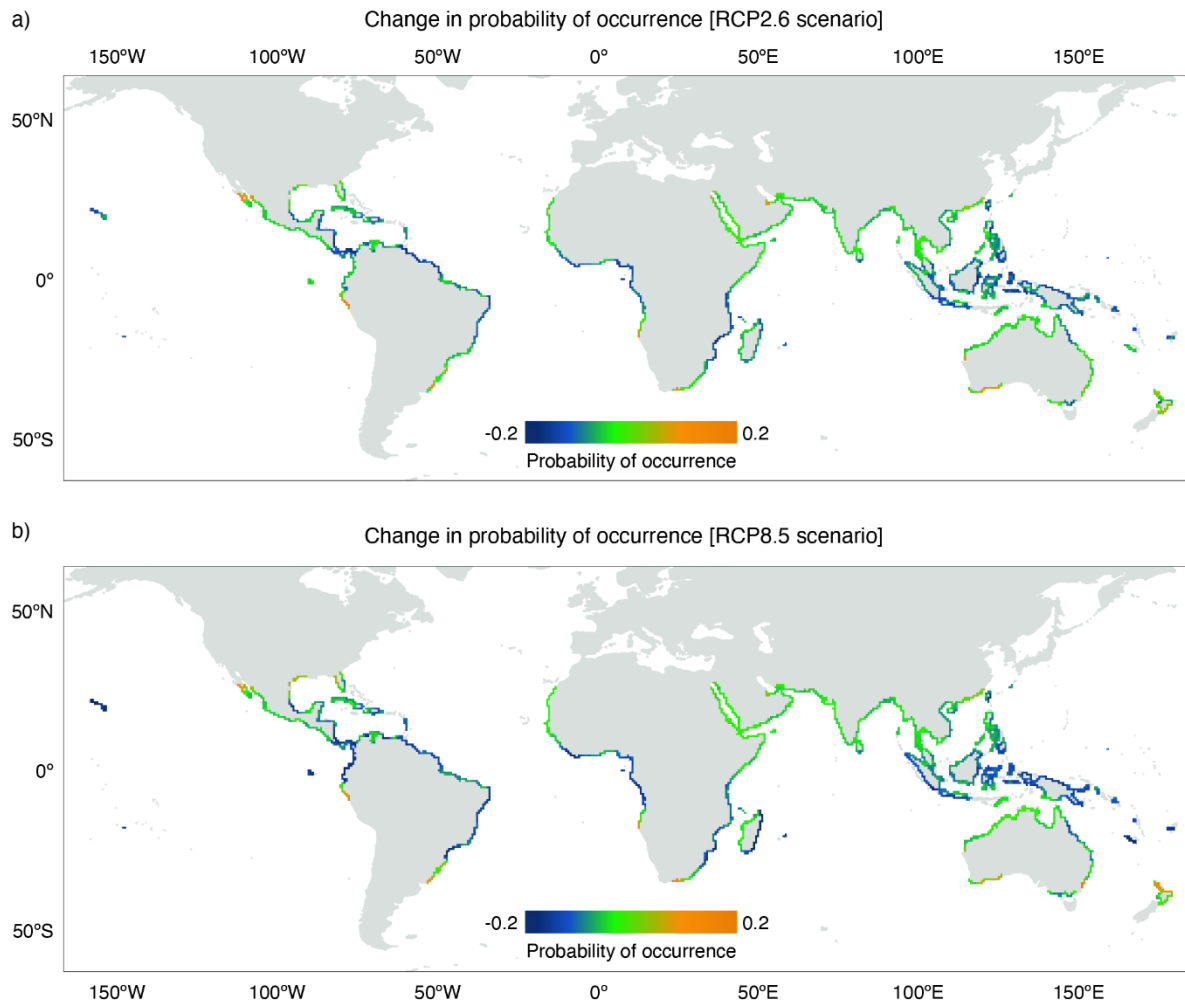
Figure 3: Change in probability of occurrence of mangrove forests (future-present) predicted for the (a) RCP 2.6 and (b) RCP 8.5 future scenarios of climate changes.

a)

Change in biomass [RCP2.6 scenario]

b)

Change in biomass [RCP8.5 scenario]
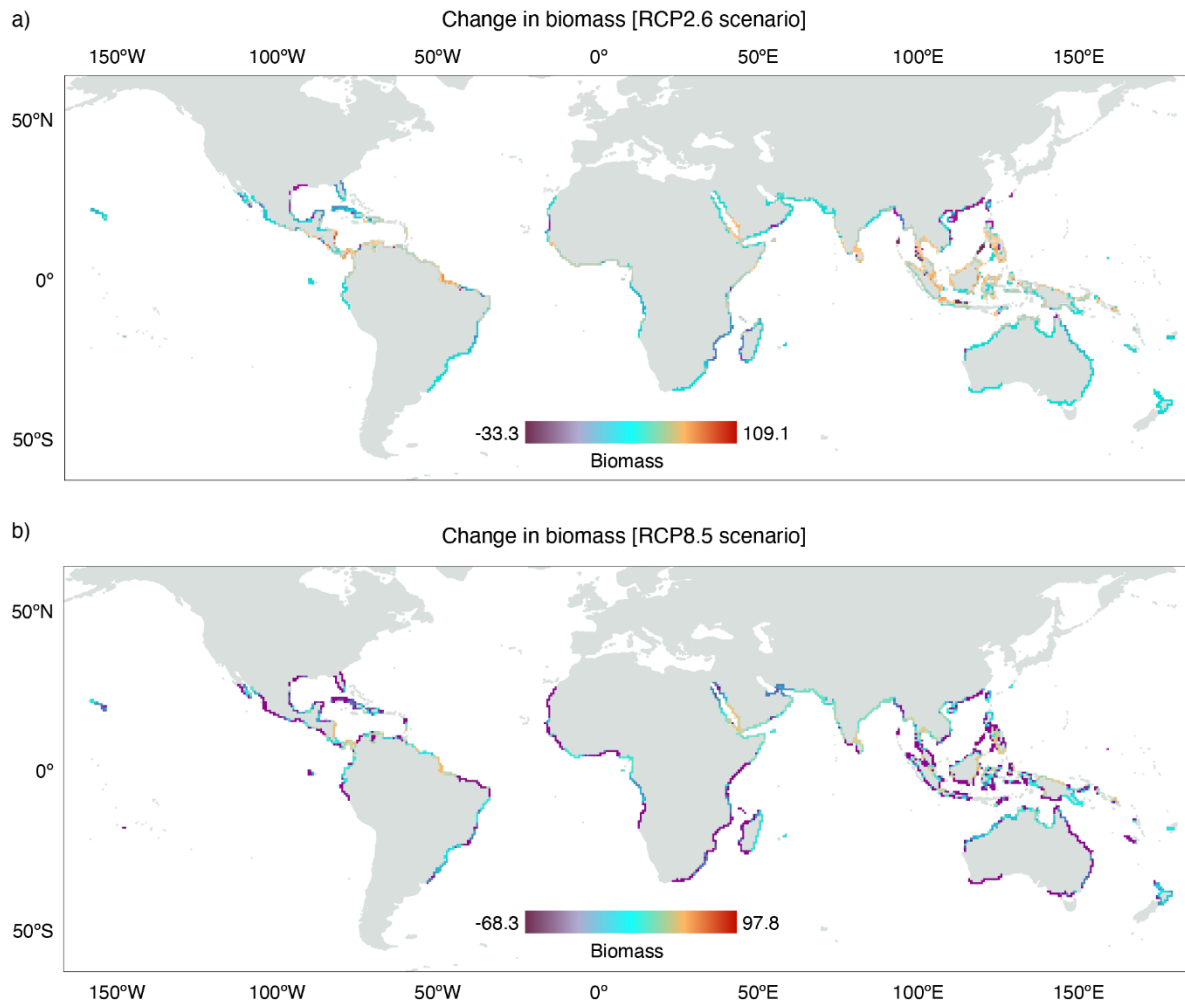
Figure 4: Change in potential biomass of mangrove forests (future-present) predicted for the (a) RCP 2.6 and (b) RCP 8.5 future scenarios of climate change.

Table 1: The AGB and Area estimated in the models for the present and future (RCP 2.6 and 8.5). The change (%) corresponds to the losses predicted in the models in both scenarios.

Variable	Present	Change (%)	
		RCP 2.6	RCP 8.5
Mean AGB (t·ha^1)	114.34	-19.75	-29.23
AGB (Pg)	2.21	-25.85	-41.20
Area (km^2)	168,063	-5.00	-14.41

Table 2: Potential distribution areas of mangrove forests predicted for the present and future scenarios of climate changes (RCP 2.6 and RCP 8.5). Areas are presented in km^2 and changes in percentage. Regions are according to Spalding et al. (2010).

Region	Area			Change			
				RCP 2.6		RCP 8.5	
	Present	RCP 2.6	RCP 8.5	fut-pres	%	fut-pres	%
North/ Central America, Caribbean	26,834	24,892	24,450	-1,942	-7.24	-2,384	-8.88
South America	30,976	29,574	24,421	-1,402	-4.53	-6,555	-21.16
Australia and New Zealand	10,746	10,525	9,563	-221.00	-2.06	-1,183	-11.01
Middle East	2,013	2,014	1,866	1.00	0.04	-126.00	-7.30
East Asia	159.71	159.3	155.25	-0.41	-0.26	-4.46	-2.79
Eastern/Southern Africa	14,976	14,535	13,333	-441.00	-2.94	-1,643	-10.97
West/Central Africa	25,986	24,340	22,242	-1,646	-6.33	-3,744	-14.41
Pacific Islands	6,798	6,205	5,139	-593.00	-8.72	-1,659	-24.40
South Asia	9,185	9,187	8,572	2.00	0.02	-613.00	-6.67
Southeast Asia	40,387	38,287	34,110	-2,100	-5.20	-4,277	-15.54
GLOBAL TOTAL (km^2)	168,063	159,718	143,851		-5.00		-14.41

Table 3: Potential biomass (Tg and t·ha^{-1}) predicted for the present and future scenarios of climate changes (RCP 2.6 and RCP 8.5).

	Present		Future										
Region			RCP 2.6						RCP 8.5				
	AGB (t·ha^{-1})	Total AGB (Tg)	AGB (t·ha^{-1})	fut-pres	%	Total AGB (Tg)	fut-pres	%	AGB (t·ha^{-1})	fut-pres	%	Total AGB (Tg)	fut-pres	%
North/ Central America, Caribbean	109.58	294.05	94.24	-15.34	-14.00	234.58	-59.47	-20.22	91.06	-18.52	-16.90	222.64	-71.41	-24.28
South America	130.6	404.55	110.99	-19.61	-15.02	328.24	-76.31	-18.86	97.29	-33.31	-25.51	237.59	-166.96	-41.27
Australia and New Zealand	94.89	101.97	72.74	-22.15	-23.34	76.55	-18.14	-17.79	62.8	-32.09	-33.82	60.06	-41.91	-41.10
Middle East	93.42	18.81	93.50	0.080	0.08	18.83	0.02	0.10	63.61	-29.81	-31.91	11.86	-6.94	-36.20
East Asia	98.81	1.58	58.79	-40.02	-40.50	0.94	-0.64	-40.51	58.79	-40.02	-40.50	0.91	-0.67	-42.23
Eastern/ Southern Africa	100.67	150.76	76.32	-24.35	-24.19	110.93	-39.83	-26.42	72.47	-28.2	-28.01	96.62	-54.14	-35.91
West/ Central Africa	105.64	274.52	76.58	-29.06	-27.51	186.4	-88.12	-32.10	71.38	-34.26	-32.43	158.76	-115.76	-42.17
Pacific Islands	113.54	77.18	95.54	-18.00	-15.85	59.28	-17.90	-23.19	92.55	-20.99	-18.49	47.56	-29.62	-38.38
South Asia	100.12	91.96	100.19	0.07	0.07	92.04	0.08	0.09	84.65	-15.47	-15.45	72.56	-19.40	-21.10
Southeast Asia	196.14	792.15	138.66	-57.48	-29.31	530.89	-261.26	-32.98	114.58	-81.56	-41.58	390.83	-401.32	-50.66
GLOBAL TOTAL	114.34	2.21	91.75		19.75	1.64		25.85	80.91		29.23	1.30		41.20

*The column of the global total in AGB is in Petagrams (Pg), and the AGB in t·ha^{-1}.

4.4 Discussion

The global mangrove forest biome is predicted by our models to decrease in aboveground biomass and area under both most extreme scenarios of future climate change, resulting in a significant loss of associated ecosystem services. The potential losses of mangrove forests due to climate change ranges from 5 to 14% in area and 26 to 42% in overall biomass on the global scale. This corresponds to absolute losses of 8,345 to 24,212 km^2 and 0.56 to 0.90 Pg of AGB. These novel predictions for global mangrove biome have high relevance for planning of conservation priorities and future habitat suitability for restoration.

Available estimates of global coverage and biomass of mangroves vary, but the results from our modelling framework (168,063 Km^2 and 2.21 Pg) are in line with those reported by other studies (155,140 km^2 and 2.82 Pg in Hutchison et al., 2014; 137,770 km^2 and 1.75 Pg in Simard et al., 2019; 130,420 km^2 and 1.90 Pg in Tang et al., 2018). The broad areas predicted for mangrove forests match known distributions, approximately 30° N e 30° S of latitude (Fig.1). These coastal wetlands are majorly distributed throughout the tropical and subtropical regions. The most significant drivers explaining distribution and AGB were minimum air and sea temperature with a relative contribution of ~50%. Our threshold for minimum and maximum air temperature were 8°C and 30°C (Fig. 2). These thresholds agree with studies that demonstrated the intolerance of mangroves to frost and low temperatures (Stuart et al., 2007; Cook-Patton et al., 2015; Devaney et al., 2020). For instance, *Rhizophora mangle* propagules from Mexico usually reach beaches and estuaries of southern Texas but die during winter freezes (Duke et al., 1998). However, *Avicennia germinans* is found in the subtropical northern Gulf of Mexico (Madrid et al., 2014). The distribution of *A. germinans* is projected to continue expanding over the next several decades in response changes in the frequency of freezing temperatures, rainfall, and the rate of sea-level rise (Osland et al., 2013; Cavanaugh et al., 2014). In general, mangrove forests thrive with temperatures of the coldest month higher than 20°C (Alongi, 2008), and they are most productive within the temperature range of 15-25°C (Hutchings & Saenger,1987). In arid environments, transpiration rates are significantly at a minimum at midday to avoid water loss, and leaf orientation is modified to minimize high leaf temperatures. Both stomatal conductance and assimilation rate are maximal at leaf temperatures ranging from 25-30°C, with a rapid decline above 35°C (Ball, 1988).

Precipitation was also identified as important to explain the models (>20%). A large part of the distribution of mangroves is in warm and humid regions (from southern Mexico to Colombia, in the Caribbean, North Brazil, and from S.E. Asia to N. Queensland). Still, they also occur in sub/semi-humid and arid areas (Blasco et al., 1984). Our models predicted a threshold of 1000 mm yr^{-1} (Fig. 2) for the potential distribution of mangrove. Range limits of precipitation between 320 and 1340 mm per year were observed to the presence and species richness (Osland et al., 2017). Complex and interrelated changes of climatic variables may lead to unpredictable environmental responses. For instance, increased precipitation in

low latitudes could be favorable to mangroves. Still, rapid increases in sediment supply combined with rainfall and land-use change may be damaging to mangrove forests (Sippo et al., 2018). There are also important interactions between temperature and precipitation as high temperatures increase evaporation rates and can result in increased salinity with consequences in species diversity, abundance, and productivity (Smith & Duke, 1987; Ball & Sobrado, 1999, Devaney et al., 2020).

The total cloud fraction was an additional important variable presenting a relative influence >10% in distribution models. The ecophysiological response to climatic conditions and the high-water use efficiency of mangroves support better growth in wet equatorial than in seasonally monsoonal or arid climates. The constant cloud cover in wet equatorial climates, prevents exposure of the forest canopy too high levels of direct sunlight, with the consequence that the leaves remain relatively cool (Clough, 1992). Clouds act as thermal regulators for the planet but are also varying due to climate change, which could contribute to increasing global warming. Global warming is altering the mechanism of cloud formation, and the absence of cloud cover could increase minimum temperatures under climate change (Brown & Caldeira, 2018).

Our estimates demonstrate that the percent loss of biomass will be three times higher than the loss of area occupied by mangroves. Plants must both grow and defend from herbivory and environmental stress to survive and reproduce. To survive under stress conditions, mangrove plants can produce antioxidant metabolites to protect the photosynthetic and cellular functions against oxidative stress (Das et al., 2015). Growth–defense tradeoffs have important ecological consequences (Huot et al., 2014). Energy can be allocated to produce secondary compounds of defense instead of investing in primary metabolism and consequently growth, decreasing in abundance. Besides, recolonization of disturbed sites may be slow and unpredictable, especially if seed sources are remote (Mckee et al., 2007). Mangroves are dominated by tree species dependent upon seedling recruitment for regeneration. Mangroves may be extremely slow to recolonize and grow, especially in harsh environments (e.g., arid, hypersaline) (Feller et al., 2003; Flower 2004, Milbrandt & Tinsley, 2006). Incapacity to recover can be produced by permanent changes in environmental conditions that inhibit recovery (e.g. subsidence, erosion, or permanent changes in hydrology) (Sippo et al., 2018).

The most relevant projected climate changes affecting mangrove distribution are increases in precipitation in the equatorial Pacific, East Africa and the Middle East, and India (Ward et al., 2016). In contrast, eastern South America and western Africa are expected to become drier (Ward et al., 2016; Osland et al., 2016). In the past, large regions in Asia, Oceania, Americas, and the Caribbean were surrounded by mangroves that formerly covered an estimated area of 188,00 km^2 in 1980 (FAO, 2007). Estimates between 2000 and 2018 report that around 150,000 km^2 persist (Hutchinson et al., 2014), 30% less than the original area. In general, Asia has the largest area of mangroves, followed by Africa, North and Central America, Oceania and South America (Sandilyan & Kathiresan, 2012; Richards & Friess, 2016; Friess et al., 2019). Asiatic mangroves have recorded the highest loss in the last few decades (Parida et al., 2014). Our estimates also anticipate future losses in area and biomass in the region due to climate change, and the decline predicted would be around 15 % and 50%, respectively (Tables 2 and 3). Studies showed that 1-13 % of mangrove forests would be lost due to climate change in the Asia/Pacific region, and it might be higher in single countries (Preston & Bathols, 2006). The most significant losses would be in Southeast Asia, followed by the Pacific islands, the West/Central Africa, and South America (see Table 2). As predicted by the present modelling framework and other studies, pronounced losses (>20%) have been reported in the Asian, Pacific regions and Central America, and limited losses in East Africa, with 8% decline between 1980 and 2005 (Lavieren et al., 2019).

Mangroves allocate much biomass into root systems (Komiyama et al., 2008) which can be aerial or belowground systems. Belowground root biomass in mangroves commonly provides up to 60% of the total tree biomass (Khan et al., 2009; Tamooh et al., 2008). This mechanism can help oxygen transport, expand water uptake, hold nutrients, and increase stability in an anoxic and waterlogged environment (Reef et al., 2010). Thus, root biomass per area in mangrove forests may be higher than the root biomass of terrestrial forests (Adame et al., 2017). Comparison of above and belowground production in forest systems at a global scale suggests a directly proportional relation (Sanchez, 2005). The decline in biomass has usually been understood as the loss of a source of carbon pools. The effect of CO_2 enrichment on mangrove forests depend on complex interactions between different physiological and environmental factors. The high temperatures increase evaporation rates and can result in

enhanced salinity with consequences for species diversity, abundance, and productivity (Smith & Duke, 1987; Ball & Sobrado, 1999).

This study focused on macroclimatic drivers of mangrove distribution and biomass such as temperature and precipitation. Climate change is also expected to have a significant impact on mangrove ecosystems through other processes not examined here, including sea-level rise (SLR), changing ocean currents and changes to the intensity of large storms (McKee et al., 2012). For example, sea-level rise is likely to have significant impacts on the future distributions of mangroves and in rates of carbon sequestration. The trends in mangrove carbon storage and stocks may be dependent on the ability of mangroves to retreat landward in the face of sea-level rise (Lovelock & Reef, 2020). However, in many coastal areas, there has been large-scale expansion along mangrove margins of urbanization and agriculture, limiting the ability of mangroves to migrate landward (Ward et al., 2016). Also, other global change factors may interact with the macroclimatic drivers examined here. For example, rising temperatures may lead to competition between mangrove species and salt marshes plants, which have C4 physiology. These plants assimilate CO_2 more efficiently than mangrove species at temperatures above 40ºC, potentially mitigating adverse effects of increased temperatures and decreased precipitation (Adam, 1993).

4.5 Conclusion

Greenhouse gas emissions are reaching new records every year, and global temperatures could rise more than double the combined limit in Paris agreement. The current commitments indicate that almost 75% of the climate pledges are partially or insufficient to contribute to reducing GHG emissions and some of these promises is improbable to be accomplished (Watson et al., 2019). This would increase the probability that climate change follows one of the more extreme pathways (i.e., RCP 8.5), which is expected to have greater negative impacts on mangrove extent and AGB. These losses could then create climate feedback as carbon stored in mangrove ecosystems is released to the atmosphere. Accordingly, it seems urgent to broadly comply with the Paris Agreement as well as protect mangroves from other direct anthropogenic threats such as deforestation, which has been increasing annually at a rate of 1-3% to give place to agriculture and aquaculture. By

identifying the region's most vulnerable to climatic impacts on mangroves, our results can be used to prioritize areas for conservation and restoration efforts.

4.6 Fundings

4.6.1 Declaration of competing interest

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

4.7 Appendix

4.7.1 Supplementary Material (Figs S1-S5)

Global loss of area and biomass of the mangrove forest biome projected for contrasting scenarios of future climate change

Lidiane P. Gouvêa[1*], Jorge Assis[2], Kyle Cavanaugh[3], Ester A. Serrão[2], Carlos F.D. Gurgel[1], Paulo A. Horta[1]

Affiliations:

[1] Phycology Laboratory, Department of Botany, Biological Sciences Center, Federal University of Santa Catarina, Florianopolis, Santa Catarina, Brazil

[2] CCMAR - Centre of Marine Sciences, University of Algarve, Faro, Portugal

[3] Department of Geography, University of California, Los Angeles, Los Angeles, California

*Corresponding author: lidi_pel@hotmail.com

Figure S1: Histogram and pair plots of environmental data utilized in distribution modelling of mangrove forests. The numbers in boxes indicate paired correlations between variables, with font size proportional to correlation strength.
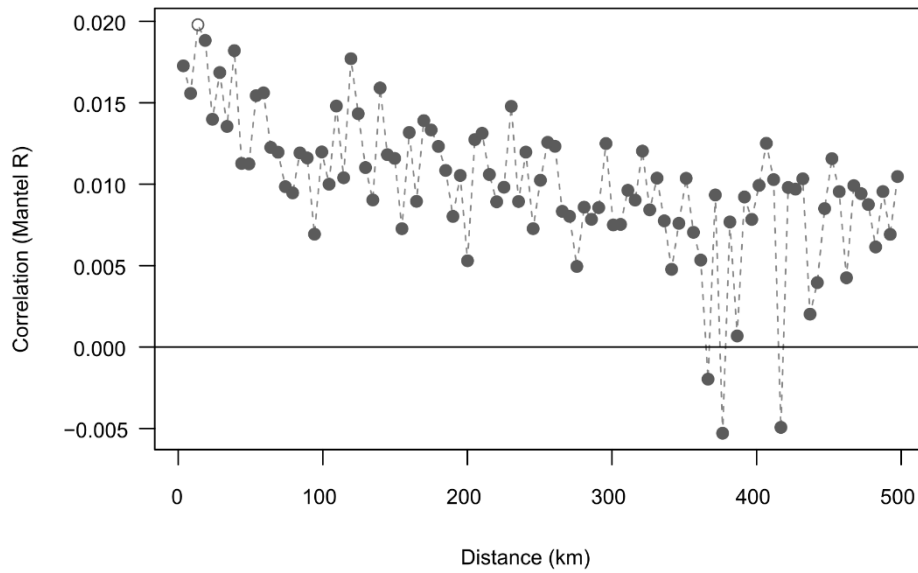
Figure S2: Spatial autocorrelation in occurrence for the mangrove species. Significant autocorrelation is indicated by closed circles.
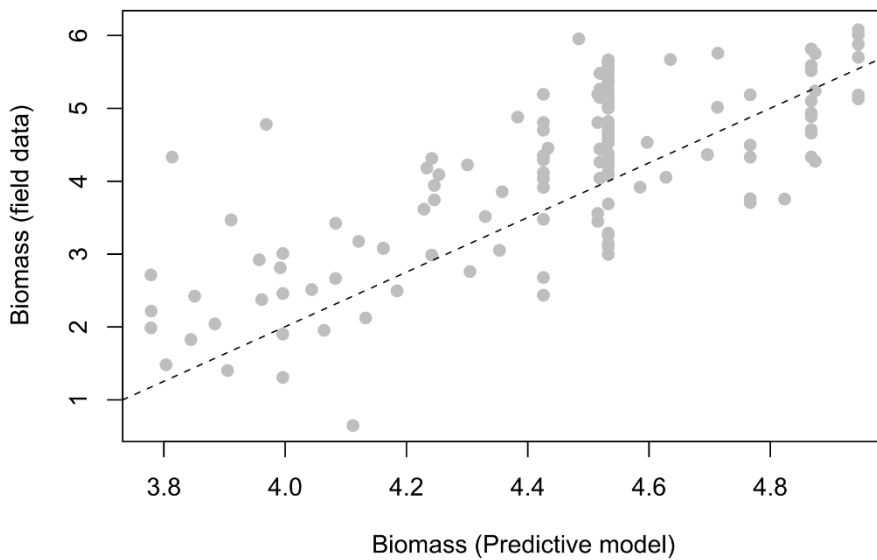
Figure S3. Comparison between observed (field) and predicted biomass, modelled with a delta-lognormal approach (R=0.587).

a

b

c
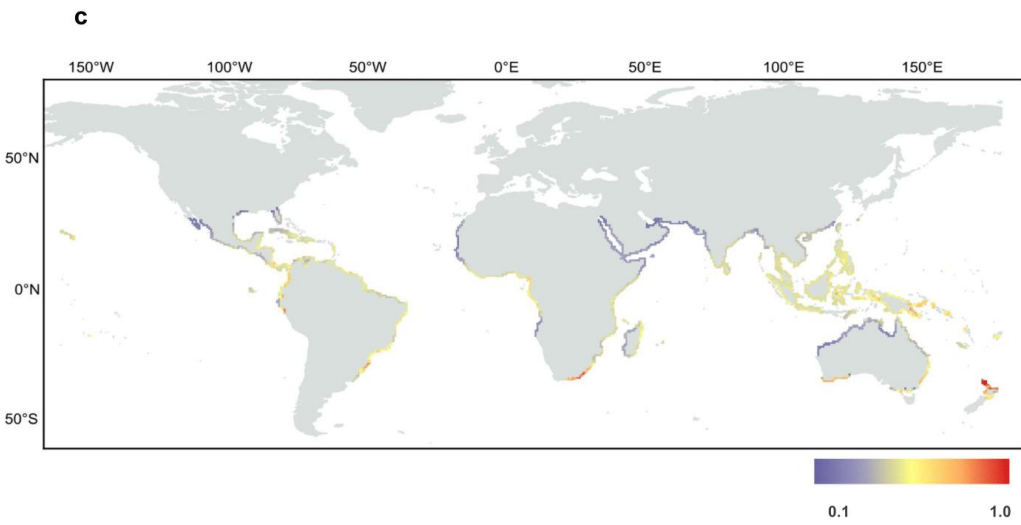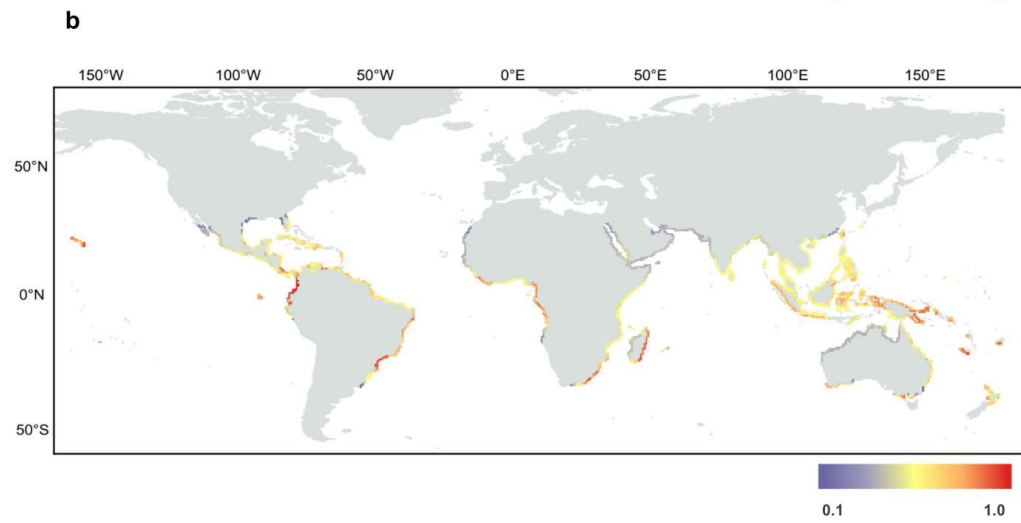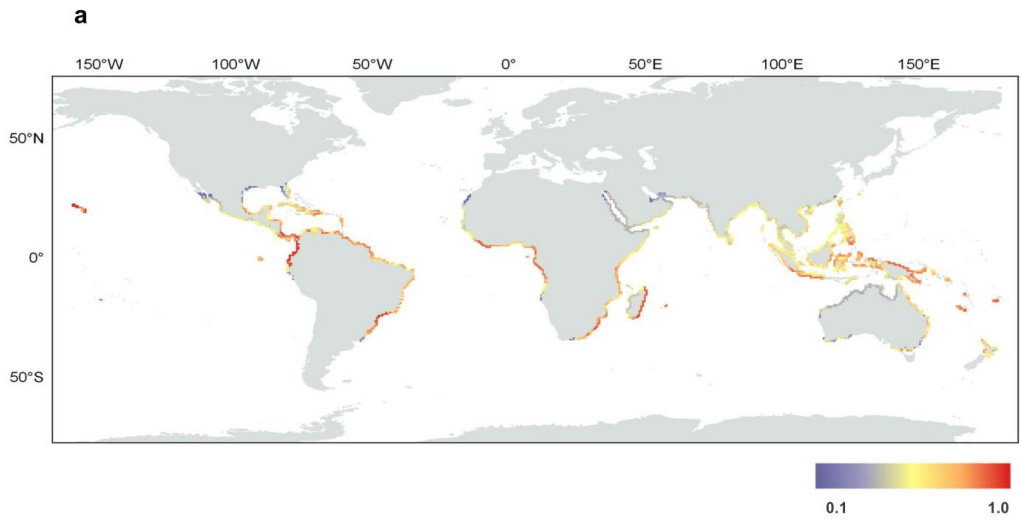
Figure S4: Potential global distribution of mangrove forests as the probability of occurrence predicted for (**a**) the present and the (**b**) RCP 2.6 and (**c**) RCP 8.5 future scenarios of climate changes.
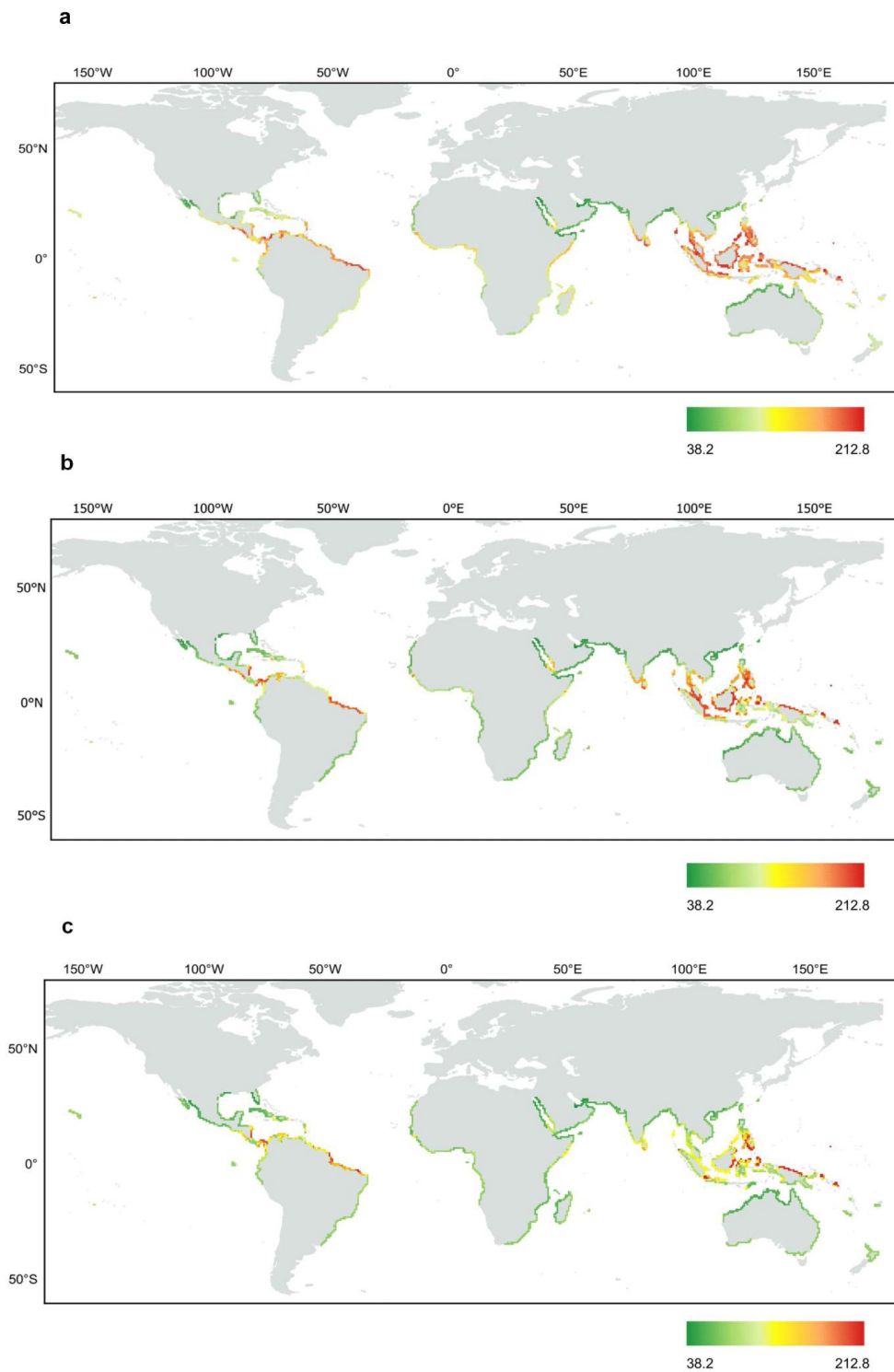
Figure S5: Potential global biomass of mangrove forests predicted for the (**a**) present and the (**b**) RCP 2.6 and (**c**) RCP 8.5 future scenarios of climate changes.

4.7.2 Supplementary Material (Table S1)

Global loss of area and biomass of the mangrove forest biome projected for contrasting scenarios of future climate change

Lidiane P. Gouvêa[1*], Jorge Assis[2], Kyle Cavanaugh[3], Ester A. Serrão[2], Carlos F.D. Gurgel[1], Paulo A. Horta[1]

Affiliations:

[1] Phycology Laboratory, Department of Botany, Biological Sciences Center, Federal University of Santa Catarina, Florianopolis, Santa Catarina, Brazil

[2] CCMAR - Centre of Marine Sciences, University of Algarve, Faro, Portugal

[3] Department of Geography, University of California, Los Angeles, Los Angeles, California

*Corresponding author: lidi_pel@hotmail.com

Table S1: Site, Longitude, Latitude, AGB (t· ha^{-1}) and references used in the biomass model for mangrove species. These data were obtained of Rovai et al. (2015) and complemented with literature data.

Site	Longitude	Latitude	AGB (t ha^{-1})	Reference
Saudi Arabia (Shuaiba)	38.29257	23.93032	18.58	Abohassan et al. (2012)
Saudi Arabia (Yanbu)	38.19444	23.97767	10.77	Abohassan et al. (2012)
Sri Lanka	8.84	6.21	240	Amarasinghe & Balasubramaniam (1992)
Sri Lanka	8.84	6.21	193	Amarasinghe & Balasubramaniam (1992)
Sri Lanka	8.84	6.21	172	Amarasinghe & Balasubramaniam (1992)
Sri Lanka	8.84	6.21	85	Amarasinghe & Balasubramaniam (1992)
Sri Lanka	8.84	6.21	71	Amarasinghe & Balasubramaniam (1992)
Sri Lanka	8.84	6.21	57	Amarasinghe & Balasubramaniam (1992)
Bu Tinah Shamal	53.1862	24.12066	38.3	Schile 2018
Bu Tinah Janoub	51.6106	25.1616	71.1	Schile 2018
Marawah Is.	53.28589	24.3062	23.1	Schile 2018
Salaam	54.40485	24.4545	25.9	Schile 2018
Eastern Mangrove	54.4036	24.45805	13.3	Schile 2018
Jubail Is.	54.46974	24.53005	15.1	Schile 2018
Jubail Is. East	54.46974	24.53005	7.3	Schile 2018
Al Shalila	54.64261	24.61807	9.2	Schile 2018
Al Khor	51.5181	25.66817	140	Schile 2018
Al Zorah	55.44756	25.42543	92.1	Schile 2018
Umm Al Quwain	55.53252	25.53943	30.8	Schile 2018
Sinnia	43.13719	14.42345	72.6	Schile 2018
Ras Al Kaimah	55.91405	25.76506	134.4	Schile 2018
Kor Al Rams	56.0075	25.87002	56.8	Schile 2018
Khalba North	56.36236	25.05329	97.9	Schile 2018
Khalba South	56.36236	25.05329	243.6	Schile 2018
Khalba East	56.36236	25.05329	144.8	Schile 2018
Khalba West	56.36236	25.05329	180.5	Schile 2018
USA (Florida)	-80.27	25.67	56	Ross et al. (2001)
China (Leizhou Bay, Guangdong)	110.1681	20.98632	39.3	Ren et al. (2010)
China (Leizhou Bay, Guangdong)	110.1681	20.98632	59.6	Ren et al. (2010)
China (Leizhou Bay, Guangdong)	110.1681	20.98632	76.4	Ren et al. (2010)

China (Leizhou Bay, Guangdong)	110.1681	20.98632	82.1	Ren et al. (2010)
China (Shenzhen)	114.06	22.54	68.07	Tam et al. (1995)
China (Shenzhen)	114.06	22.54	10.58	Tam et al. (1995)
China (Shenzhen)	114.06	22.54	8.49	Tam et al. (1995)
China (Dongzhai Bay)	110.6185	19.92699	38.53	Liao et al. (1999)
China (Dongzhai Bay)	110.6185	19.92699	20.01	Liao et al. (1999)
China (Yingluo Bay)	109.7513	21.57212	40.01	Wang et al. (2013)
China (Yingluo Bay)	109.7536	21.56448	153.23	Wang et al. (2013)
China (Yingluo Bay)	109.7642	21.56915	97.17	Wang et al. (2013)
China (Yingluo Bay)	109.7676	21.5545	148.71	Wang et al. (2013)
China (Yingluo Bay)	109.7753	21.53656	270.59	Wang et al. (2013)
Japan (Okinawa)	127.68	26.19	108.1	Suzuki & Tagawa (1983)
Japan (Okinawa)	127.68	26.19	97.6	Suzuki & Tagawa (1983)
Japan (Okinawa)	127.68	26.19	78.6	Suzuki & Tagawa (1983)
Japan (Okinawa)	127.68	26.19	75.1	Khan et al. (2004, 2007)
Japan (Manko Wetland, Okinawa)	127.68	26.19	109.28	Hoque et al. (2011)
India (Andaman Island)	92.75	12.5	124	Mall et al. (1991)
India (Andaman Island)	92.75	12.5	214	Mall et al. (1991)
Mozambique (Inhaca island)	32.91468	-26.0361	107	Boer (2000)
Kenya (Gazi Bay)	39.52	-4.41	106.7	Kairo et al. (2008)
Kenya (Gazi Bay)	39.52	-4.41	11.7	Kairo et al. (2009)
Kenya (Gazi Bay)	39.52	-4.41	6.7	Kairo et al. (2009)
Kenya (Gazi Bay)	39.52	-4.41	3.7	Kairo et al. (2009)
Kenya (Gazi Bay)	39.52	-4.41	20.25	Kairo et al. (2009); Kairo et al. (2001); Bosire et al. (2003, 2006)
Kenya (Gazi Bay)	39.52	-4.41	452.02	Bosire et al. (2003); Kirui et al. (2006)
Kenya (Gazi Bay)	39.52672	-4.41423	131.6	Lang'at (2008)
Kenya Ramisi estuary)	39.43615	-4.57115	16.65	Lang'at (2008)
South Africa	31.03563	-29.808	74.67	Steinke et al. (1995)
South Africa	31.03563	-29.808	19.82	Steinke et al. (1995)
Thailand (Ranong Southern)	98.61	9.95	281.2	Tamai et al. (1986)
Thailand (Satun Southern)	100.16	6.59	92.2	Komiyama et al. (2000)
Thailand (Trat)	102.5717	12.19254	1.91	Okimoto et al. (2013)
Thailand (Southern Pang-nga)	98.52	8.44	62.2	Poungparn et al. (2003); Komiyama et al. (2008)
Thailand (Trat Eastern)	102.52	12.24	142.2	Poungparn et al. (2003); Komiyama et al. (2008)
Malaysia (Kuala Sepetang, Matang)	100.617	4.836569	214.32	Jin-Eong et al. (1995)
Micronesia (Airai, Palau)	134.5392	7.35202	174	Kauffman et al. (2011)

Micronesia (Airai, Palau)	134.5395	7.352941	212	Kauffman et al. (2011)
Micronesia (Airai, Palau)	134.5398	7.354299	289	Kauffman et al. (2011)
Micronesia (Yap)	138.1275	9.588354	251	Kauffman et al. (2011)
Micronesia (Yap)	138.1275	9.587323	456	Kauffman et al. (2011)
Micronesia (Yap)	138.1274	9.586271	383	Kauffman et al. (2011)
Indonesia (Java)	109.2	-7.28	93.73	Sukardjo & Yamada (1992)
Indonesia (Halmahera)	128.49	1.31	436.4	Komiyama et al. (1988)
Indonesia (Halmahera)	128.49	1.31	406.6	Komiyama et al. (1988)
Indonesia (Halmahera)	128.49	1.31	356.8	Komiyama et al. (1988)
Indonesia (Halmahera)	128.49	1.31	299.1	Komiyama et al. (1988)
Indonesia (Halmahera)	128.49	1.31	178.2	Komiyama et al. (1988)
Indonesia (Halmahera)	128.49	1.31	169.1	Komiyama et al. (1988)
Indonesia (Halmahera)	128.49	1.31	216.8	Komiyama et al. (1988)
Indonesia (East Sumatra)	103.8029	0.018566	89.68	Kusmana et al. (1992)
Indonesia (East Sumatra)	103.8029	0.018566	42.94	Kusmana et al. (1992)
Indonesia (East Sumatra)	103.8029	0.018566	75.99	Kusmana et al. (1992)
Indonesia (East Sumatra)	103.8029	0.018566	178.81	Kusmana et al. (1992)
Indonesia (East Sumatra)	103.8029	0.018566	279.03	Kusmana et al. (1992)
Indonesia (East Sumatra)	103.8029	0.018566	40.7	Kusmana et al. (1992)
Brazil (Bertioga, São Paulo)	-46.2063	-23.897	42.3	Lamparelli (1995)
Brazil (Bertioga, São Paulo)	-46.1452	-23.8165	59.7	Lamparelli (1995)
Brazil (Babitonga Bay)	-48.7507	-26.2045	37.2	Cunha et al. (2006)
Brazil (Itamaracá/PE)	-34.85	-7.8	104.79	Medeiros & Sampaio (2008)
Brazil (Potengi Estuary)	-35.2069	-5.76748	85.96	Ramos-Silva et al. (2007)
Brazil (Sepetiba Bay, Rio de janeiro)	-43.59	-23.02	65.4	Silva (1988); Silva et al. (1991, 1998)
Brazil (Bertioga, São Paulo)	-46.21	-23.9	51.54	Soares & Schaeffer-Novelli (2005)
Brazil (Sepetiba Bay, Rio de Janeiro)	-43.59	-23.02	166.58	Soares & Schaeffer-Novelli (2005)
Colombia (Rancheria river delta)	-72.8926	11.54039	70.98	Vélez & Polanía (2007)
Colombia (Rancheria river delta)	-72.9014	11.55347	26.8	Vélez & Polanía (2007)
Dominican Republic	-69.67	19.17	233	Sherman et al. (2003)
Panama (Bocas del Toro)	-82.2639	9.352515	59.5	Lovelock et al. (2005)
Panama	-78.1777	8.463944	279.4	Golley et al. (1969, 1975)
Panama (Gulf of Monitjo)	-81.0778	7.930253	105.7	Gross et al. (2014)

Panama (Gulf of Monitjo)	-81.0778	7.930253	335.3	Gross et al. (2014)
Panama (Gulf of Monitjo)	-81.0778	7.930253	110.8	Gross et al. (2014)
Panama (Gulf of Monitjo)	-81.0778	7.930253	132.7	Gross et al. (2014)
Panama (Gulf of Monitjo)	-81.0778	7.930253	164.2	Gross et al. (2014)
Panama (Gulf of Monitjo)	-81.0778	7.930253	76.2	Gross et al. (2014)
Panama (Gulf of Monitjo)	-81.0778	7.930253	248.7	Gross et al. (2014)
Panama (Gulf of Monitjo)	-81.0778	7.930253	267.2	Gross et al. (2014)
Panama (Gulf of Monitjo)	-81.0778	7.930253	139.1	Gross et al. (2014)
Panama (Bocas del Toro)	-82.2093	9.318016	22.2	Lovelock et al. (2005)
Panama (Bocas del Toro)	-82.0865	9.17821	8.3	Lovelock et al. (2005)
Panama (Bocas del Toro)	-82.2477	9.268186	194.3	Lovelock et al. (2005)
Tobago (Bon Accord Lagoon)	-60.8243	11.16651	180	Juman (2005)
Tobago (Bon Accord Lagoon)	-60.8243	11.16651	94	Juman (2005)
Tobago (Bon Accord Lagoon)	-60.8243	11.16651	215	Juman (2005)
Tobago (Bon Accord Lagoon)	-60.8243	11.16651	102	Juman (2005)
Tobago (Bon Accord Lagoon)	-60.8243	11.16651	118	Juman (2005)
Tobago (Bon Accord Lagoon)	-60.8243	11.16651	20	Juman (2005)
Tobago (Bon Accord Lagoon)	-60.8243	11.16651	259	Juman (2005)
USA (Shark River, Florida)	-80.9642	25.40972	108	Castaneda-Moya et al. (2013)
USA (Shark River, Florida)	-81.0322	25.37687	95.4	Castaneda-Moya et al. (2013)
USA (Shark River, Florida)	-81.0778	25.36441	162.2	Castaneda-Moya et al. (2013)
USA (Taylor River, Florida)	-80.5244	25.23246	4.4	Castaneda-Moya et al. (2013)
USA (Shark River, Florida)	-81.0506	25.37	247.59	Chen & Twilley (1999)
USA (Shark River, Florida)	-81.0506	25.37	251.85	Chen & Twilley (1999)
USA (Shark River, Florida)	-81.0506	25.37	120.87	Chen & Twilley (1999)
USA (Shark River, Florida)	-81.0506	25.37	79.68	Chen & Twilley (1999)
Mexico (Boca Chica)	-92.33	18.67	135	Day-Jr et al. (1987)
Mexico (Estero Pargo)	-92.33	18.67	120	Day-Jr et al. (1987)
French Guiana	-52.32	4.87	315	Fromard et al. (1998)

French Guiana	-52.32	4.87	188.6	Fromard et al. (1998)
French Guiana	-53.25	5.42	180	Fromard et al. (1998)
French Guiana	-53.25	5.42	122.2	Fromard et al. (1998)
French Guiana	-52.32	4.87	71.8	Fromard et al. (1998)
French Guiana	-53.17	5.5	35.1	Fromard et al. (1998)
French Guiana	-53.25	5.42	31.5	Fromard et al. (1998)
French Guiana (Sinnamary estuary)	-53.25	5.416667	56.6	Fromard et al. (2004)
French Guiana (Sinnamary estuary)	-53.25	5.416667	11.42	Fromard et al. (2004)
French Guiana (Sinnamary estuary)	-53.25	5.416667	61.4	Fromard et al. (2004)
French Guiana (Sinnamary estuary)	-53.25	5.416667	50.2	Fromard et al. (2004)
French Guiana (Sinnamary estuary)	-53.25	5.416667	73.1	Fromard et al. (2004)
French Guiana (Sinnamary estuary)	-53.25	5.416667	32.39	Fromard et al. (2004)
French Guiana (Sinnamary estuary)	-53.25	5.416667	14.58	Fromard et al. (2004)
French Guiana (Sinnamary estuary)	-53.25	5.416667	180	Fromard et al. (2004)
French Guiana (Sinnamary estuary)	-53.25	5.416667	214.4	Fromard et al. (2004)
French Guiana (Sinnamary estuary)	-53.25	5.416667	228.84	Fromard et al. (2004)
French Guiana (Sinnamary estuary)	-53.25	5.416667	431.9	Fromard et al. (2004)
French Guiana (Sinnamary estuary)	-53.25	5.416667	122.2	Fromard et al. (2004)
French Guiana (Sinnamary estuary)	-53.25	5.416667	110	Fromard et al. (2004)
French Guiana (Sinnamary est.)	-53.25	5.416667	77.6	Fromard et al. (2004)
Australia	153.1379	-27.3998	341	Mackey (1993)
Australia	153.1379	-27.3998	162	Mackey (1993)
Australia	153.1379	-27.3998	110	Mackey (1993)
Australia (Kooragang Island)	151.76	-32.84	21.8	Murray (1985)
Australia (Gosford)	151.76	-32.84	21.7	Murray (1985)

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5 CONCLUSÃO GERAL

Análises atuais mostram que 75% das promessas climáticas, no Acordo de Paris (2020-2030), são parciais ou totalmente insuficientes para contribuir na redução das emissões, sendo que algumas provavelmente não serão cumpridas (WATSON *et al.,* 2019). As emissões de gases de efeito estufa atingiram novos recordes no ano passado, e as temperaturas mundiais podem subir mais do que o dobro do limite combinado do acordo de Paris (ALLEN *et al.,* 2019). Isso aumentaria a probabilidade de que as mudanças climáticas sigam um dos caminhos mais extremos (ou seja, RCP 8.5), que deverá ter impactos negativos na extensão e AGB das florestas de *Sargassum* e mangues, como evidenciado neste estudo. O Brasil comprometeu-se em reduzir as emissões de gases de efeito estufa em 37% até 2025, estendendo esta redução em 43% até 2030. Porém, o cenário é outro, o descumprimento das políticas de controle do desmatamento e o apoio político às práticas agrícolas predatórias impossibilitam a realização de metas consistentes pelo Brasil (ROCHEDO *et al.,* 2018).

A demanda urgente por mitigação de CO_2 e as ameaças de crescente urbanização costeira representam argumentos para se destacar o *Sargassum* bentônico e flutuante, como um alvo primário para iniciativas de conservação, manejo e eventual restauração em um contexto global. Com base nos resultados apresentados neste trabalho, concluímos que a macroalga *Sargassum* tem o potencial de fazer contribuições ecologicamente significativas para o estoque de carbono a nível global. Além disso, o entendimento dos fatores ambientais no crescimento e acúmulo de biomassa de *Sargassum*, bem como o Ferro apresentando grande influência na abundância observada, fornece novos caminhos para o manejo/produção desta macroalga. Nosso estudo reforça a importância da inclusão das macroalgas nas iniciativas internacionais de carbono azul, que é focado na mitigação das mudanças climáticas por meio da conservação e restauração dos ecossistemas costeiros e marinhos (KRAUSE-JENSEN e DUARTE, 2016).

Por outro lado, declínios localizados das espécies de florestas submersas têm sido relatados ao longo da costa brasileira e atribuídos a estressores locais (MARTINS *et al.,* 2012; GORMAN *et al.,* 2020). A costa brasileira apresenta grande variabilidade de condições ambientais, sendo um bom sistema de modelo para entender os processos de deslocamento e prever as consequências de futuras mudanças climáticas. A região de Santa Catarina é um

importante zona de transição biogeográfica, onde um número considerável de espécies marinhas atinge seus limites de distribuição. Neste contexto, nosso experimento laboratorial mostrou que a espécie bentônica, *S. cymosum*, presente em seus limites de distribuição, como no Sul do Brasil, poderão perder biomassa principalmente se o clima do planeta seguir o cenário de RCP 6.0 e 8.5 até 2100.

Além disso, estas previsões podem afetar todos os ecossistemas marinhos e costeiros, sendo que um dos mais ameaçados são as florestas de mangues. Cerca de 35–50% destas florestas desapareceram nos últimos 50 anos (DONATO *et al.,* 2011). Elas atuam como "amortecedores" dos eventos climáticos extremos resultando em redução do impacto ambiental. Aqui, utilizando variáveis ambientais para previsões futuras, nós chegamos a resultados diferentes dos previstos até agora (LOVELOCK e REEF, 2019). Isso mostra que, mesmo com expansão dos mangues em alguns locais, a nível global este saldo pode ser negativo com sérias implicações para o sequestro de carbono. Essas perdas poderiam, então, criar um *feedback* climático à medida que o carbono armazenado nos ecossistemas de mangue é liberado para a atmosfera (MCLEOD *et al.,* 2011; HOWARD *et al.,* 2017).

Ao identificar as regiões mais vulneráveis aos impactos climáticos das florestas marinhas e costeiras, nossos resultados podem ser usados para priorizar áreas para esforços de conservação, restauração e incluir adequação futura de habitat para as espécies. Além disso, estas florestas devem ter suas áreas e biomassa continuamente monitorados para fornecer informações sobre fontes de carbono.

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