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Marina Nasri Sissini

Algas calcárias nos recifes brasileiros – diversidade, macroecologia e conservação

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Tese submetida ao Programa de Pós-Graduação em Ecologia da Universidade Federal de Santa Catarina para a obtenção do título de doutor em Ecologia.
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O presente trabalho em nível de doutorado foi avaliado e aprovado por banca examinadora composta pelos seguintes membros:

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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 obtido pelo Programa de Pós-Graduação em Ecologia da Universidade Federal de Santa Catarina.

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RESUMO

As algas calcárias estão presentes em praticamente todos os ambientes marinhos e no Atlântico Sul Ocidental têm revelado importantes papéis no processo de construção e manutenção dos ambientes recifais. O entendimento dos padrões atuais de distribuição destes organismos, assim como a história biogeográfica do grupo nos permitem refletir e teorizar sobre como esses organismos fotossintetizantes responderão às emergentes e intensas modificações dos ecossistemas marinhos e se colocam como um passo importante para o delineamento de estratégias de conservação destes organismos e dos ambientes a eles relacionados. Contudo, pouco se sabe sobre a biodiversidade, ecologia e evolução destes organismos que habitam e constroem boa parte dos recifes brasileiros. Diante disto, foram avaliados aspectos ecológicos e históricos envolvidos na biogeografia destes organismos. No **Capítulo 1**, foram abordados os aspectos ecológicos (abióticos) relacionados aos padrões de distribuição a partir da quantificação da riqueza de espécies de algas calcárias para seis ecorregiões do Atlântico Sul Ocidental através de métodos de delimitação de espécies baseados em sequências de DNA. A partir desta compilação, foram verificadas as principais variáveis ambientais responsáveis pelos padrões de riqueza de espécies e β-diversidade. Foram encontradas 79 unidades taxonômicas operacionais moleculares (MOTU) dentro das três principais ordens de algas calcárias (Sporolithales, Corallinales e Hapalidiales) para o Atlântico Sul Ocidental tropical e temperado quente. As diferenças nos padrões de riqueza de espécies entre as ecorregiões pôde ser explicada pela temperatura superficial do mar, concentração de nutrientes e velocidade das correntes marinhas. A ecorregião Leste se destacou pela maior riqueza, maior β-diversidade e por abrigar espécies únicas. Já no **Capítulo 2**, foram explorados aspectos históricos envolvidos no processo evolutivo das algas calcárias procurando compreender a origem das espécies que atualmente ocorrem nos recifes brasileiros. Para isso, foi construída a filogenia global de Sporolithales, e sua posterior calibração através da datação de fósseis. A estimativa do estado ancestral, assim como a teoria de tectônica de placas e reconstruções paleoceanográficas subsidiaram nossas discussões. Através dos métodos de delimitação de espécies baseados em sequências de DNA, foram encontradas 23 MOTU de Sporolithales, distribuídas em nove domínios marinhos, sendo o Atlântico Tropical o mais rico em espécies. Nossos resultados mostraram que as espécies de *Sporolithon* que ocorrem no Atlântico Sul Ocidental tiveram origem através de rotas e tempos diferentes e o Caribe pode ter atuado como centro de dispersão. Ao longo do tempo geológico, identificamos o Sistema Rio Grande–Walvis Ridge e o fechamento do Istmo do Panamá como as principais barreiras biogeográficas relacionadas aos mecanismos evolutivos das Sporolithales. Os resultados encontrados nos **Capítulos 1 e 2** revelam importantes questões práticas para o monitoramento e estratégias de conservação dos recifes costeiros, oceânicos e mesofóticos. Desta maneira, no **Capítulo 3**, foi apresentada na forma de uma carta a necessidade e urgência em se proteger as algas calcárias e os ambientes por ela formados considerando as ameaças do antropoceno, especialmente aquelas relacionadas à exploração e queima de combustíveis fósseis. Frente ao desafio de conservação e uso sustentável dos oceanos promovido pelas Nações Unidas para a Década de Ciência dos Oceanos, o presente trabalho fornece novos argumentos para subsidiar o alcance deste objetivo.

Palavras-chave: Recifes biogênicos. Rodolitos. Biogeografia. Métodos de delimitação de espécies.

ABSTRACT

Coralline red algae (CRA) are present in almost all marine environments and in the Southwestern Atlantic (SWA) has proved to be key players in the construction and maintenance of reef environments. The understanding of the current patterns of distribution of these organisms, as well as the biogeographic history of the group, allows us to reflect and theorize on how these photosynthetic organisms will respond to the emerging and intense changes in marine ecosystems subsidizing robust conservation strategies. However, the biodiversity, ecology and evolution of these organisms that inhabit and build the Brazilian reefs is little known. Thus, ecological, and historical aspects involved in the biogeography of CRA were evaluated in the present study. In the **Chapter 1**, the ecological aspects (abiotic) related to the distribution patterns were addressed from the quantification of the species richness of CRA for six ecoregions in the SWA through species delimitation methods based on DNA sequences. From this compilation, the main environmental drivers responsible for the species richness and β-diversity patterns were verified. Seventy-nine molecular operational taxonomic units (MOTU) were found within the three main orders of CRA (Sporolithales, Corallinales and Hapalidiales) for the tropical and warm temperate provinces in the SWA. The differences in species richness patterns between ecoregions could be explained by the sea surface temperature, nutrients concentration and water current velocity. The Eastern ecoregion stood out for its highest species richness, β-diversity and harbouring unique species. In **Chapter 2**, historical aspects involved in the evolutionary process of CRA were explored to understand the origin of species that currently occur in the Brazilian reefs. For this, the global phylogeny of Sporolithales was built, and its subsequent calibration through fossils. Reconstruction methods of ancestral distribution as well as plate tectonics theory, and palaeoceanographic reconstructions supported our discussions. Through species delimitation methods based on DNA sequences, 23 MOTU of Sporolithales were found, distributed in nine marine realms and the Tropical Atlantic was the most species richness. Our results showed that *Sporolithon* species occurring in the SWA originated at different routes and times, and the Caribbean may have acted as a center of dispersion. Over geological time, we identified the Rio Grande-Walvis Ridge System and the closing of the Isthmus of Panama as the main biogeographic barriers related to the evolutionary mechanisms of the Sporolithales. The results found in **Chapters 1** and **2** reveal important practical issues for monitoring and conservation strategies for coastal, ocean and mesophotic reefs. Thus, in **Chapter 3**, was presented in a letter the need and urgency to protect CRA and the environments formed by them considering the threats from the anthropocene, especially those related to the exploration and burning of fossil fuels. Faced with the challenge of conservation and sustainable use of the oceans promoted by the United Nations for the Decade of Science of the Oceans, the present work provides new arguments to subsidize the achievement of this goal.

Keywords: Biogenic reefs. Rhodoliths. Biogeography. Species delimitation methods.

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1 INTRODUÇÃO GERAL

Os recifes biogênicos estão entre as formações biológicas mais diversas e ameaçadas do planeta, fornecendo serviços ecossistêmicos de alto valor e funções ainda subestimadas para as regiões costeiras (WORM et al., 2006; PAOLI et al., 2016; AMADO-FILHO et al., 2017; HALL-SPENCER; HARVEY, 2019). Em todo o mundo, as perdas de riqueza nos recifes foram identificadas, quantificadas e monitoradas considerando o branqueamento de corais ou mudanças na composição dos ambientes, outrora dominados por corais que passam a ser dominados por macroalgas (BELLWOOD et al., 2004; MCMANUS; POLSENBERG, 2004; MALIAO; TURINGAN; LIN, 2008). Com o avanço da caracterização da estrutura de comunidades destas formações, principalmente no Atlântico Sul (MOURA et al., 2016; MAZZEI et al., 2017; AUED et al., 2018; BASTOS et al., 2018), tem-se revelado particularidades, como formações recifais únicas (chapeirões, LEÃO; KIKUCHI; TESTA, 2003; montes coralinos, GUABIROBA et al., submetido) e grande participação das algas calcárias no processo de construção e manutenção destes recifes[1] (revisão em HORTA et al., 2016; MAZZEI et al., 2017; AUED et al., 2018; BASTOS et al., 2018). Estes produtores primários muitas vezes são os majoritários no processo de formação dos recifes modernos, como é o caso do Atol das Rocas (GHERARDI; BOSENCE, 2001), em outros casos atuam como cimentadores, conferindo rigidez e volume à estrutura recifal (BOSENCE, 1983; RIDING, 2002).

No Atlântico sul ocidental (ASO), as algas calcárias[2] estão presentes em praticamente

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[1] Conceituar recife é bastante audacioso e precisa ser feito sob a perspectiva dos diferentes organismos que os estruturam e contribuem para seus papéis biogeoquímicos. O termo recife engloba um conjunto de estruturas marinhas biosedimentares resultantes de eventos evolutivos em diferentes escalas de espaço e tempo. Muitos autores definem recifes como sendo "estruturas confinadas construídas pelo crescimento ou atividade metabólica de organismos aquáticos bentônicos sésseis" (KIESSLING, 2003). No entanto, modernos bancos de corais de águas frias e profundas também podem ser descritos como recifes (ROBERTS et al., 2006; KIESSLING, 2009), mesmo que não se encaixem na definição genérica. Riding (2002) destacou as falhas e consequências de definir recifes com base apenas em aspectos quantitativos superficiais ao invés de características funcionais essenciais. A comparação baseada em aspectos biológicos perde informações valiosas sobre características e grande diversidade de tipos de recifes. Por este motivo, acreditamos que a classificação estrutural (física) dos recifes biogênicos proposta por Riding (2002) é a mais abrangente para classificar os recifes biogênicos do Atlântico Sul Ocidental, incluindo os bancos de rodolitos.

[2] No presente trabalho, o termo “algas calcárias” é empregado para o grupo de algas vermelhas que depositam carbonato de cálcio na sua parede celular (em inglês usamos *coralline red algae*, CRA). A deposição do carbonato de cálcio nestas algas pode ocorrer: 1) por todo o talo, e estas algas são chamadas de algas calcárias não articuladas ou não geniculadas e, 2) de maneira intercalada, apresentando regiões não calcificadas entre porções calcificadas do talo e estas algas são conhecidas como algas calcárias articuladas ou geniculadas. Em relação às algas calcárias não articuladas, estas são classificadas quanto ao seu hábito de vida, podendo: 1) crescer aderidas ao substrato como em rochas, conchas, corais, e são chamadas então, de incrustantes (*crustose coralline algae* ou *encrusting calcareous algae*) ou, 2) estar soltas no substrato inconsolidado, estes nódulos calcários são comumente conhecidos como rodolitos (*rhodoliths*). Nas últimas duas décadas, a sistemática do grupo vem se modificando, especialmente pelo uso de ferramentas moleculares. Atualmente, as algas calcárias estão dentro da subclasse

todos os ambientes marinhos (Figura 1), desde recifes rasos a mesofóticos, recifes colunares (chapeirões), recifes (costões) rochosos e até mesmo em substratos não consolidados como nódulos livres, conhecidos como rodolitos (GHERARDI; BOSENCE, 2001; AMADO-FILHO et al., 2012; PEREIRA-FILHO et al., 2012; MEIRELLES et al., 2015; AUED et al, 2018; BASTOS et al., 2018). Baseados na distribuição atualmente conhecida, foram estimados cerca de 230.000 km^2 de área potencial para ocorrência de rodolitos ao longo do litoral brasileiro (CARVALHO et al., 2020a), para o qual já se tem o registro dos bancos mais extensos do mundo (AMADO-FILHO et al., 2012).

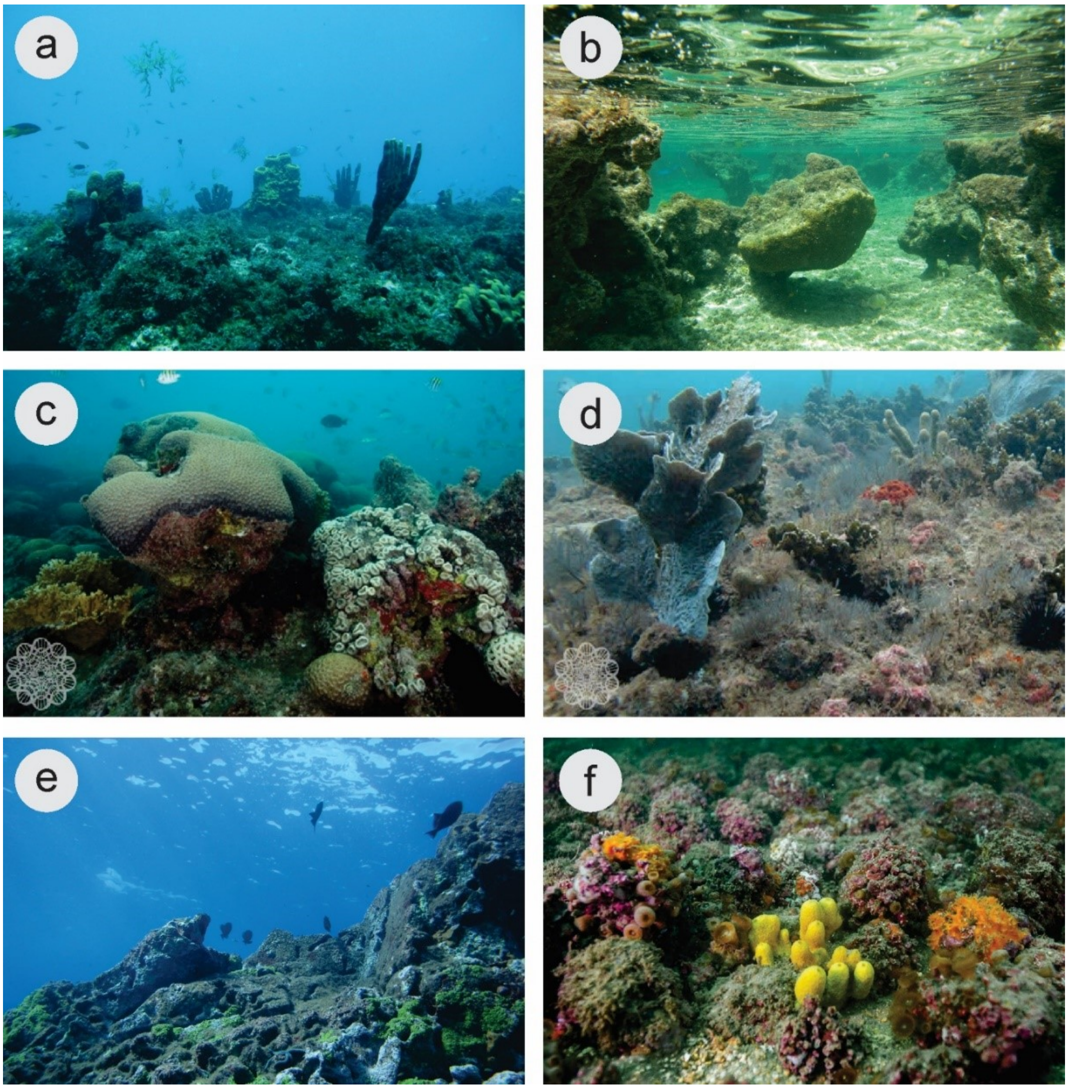

Figura 1. Exemplo de recifes costeiros e oceânicos ao longo do litoral brasileiro. (**a)** Pedra do Silva, no Rio Grande do Norte; (**b)** Atol das Rocas; (**c)** Abrolhos, Bahia; **(d)** Guarapari, Espírito

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Corallinophycidae a qual é morfologicamente caracterizada por tampões protéicos das conexões celulares (*pit plugs*) em forma de domo e talo mineralizado pela deposição de calcita (LE GALL; SAUNDERS, 2007). São reconhecidas cinco ordens dentro desta subclasse: Rhodogorgonales, Sporolithales (LE GALL et al., 2010), Corallinales, Hapalidiales (NELSON et al., 2015) e Corallinapetrales (JEONG et al., 2021), tendo apenas as quatro últimas representantes de “algas calcárias”.

Santo; **(e)** Ilha da Trindade; **(f)** Ilha do Arvoredo, Santa Catarina. [Créditos: (a, b, e) M.N. Sissini; (c, d) SISBIOTA Mar; (f) E.O. Bastos].

Contudo, o papel funcional e a biodiversidade das algas calcárias não articuladas nos recifes são aspectos influenciados por condições físicas (ADEY; STENECK, 2001; WILSON et al., 2004), biogeoquímicas (BJORK et al., 1995; DELGADO; LAPOINTE, 1994; WILSON et al., 2004) e biológicas (STENECK, 1983) que variaram dramaticamente desde as crostas de algas calcárias ancestrais que apresentam registros desde o Cambriano (*c.* 540 milhões de anos, Ma, JOHNSON; HOEG, 1961; STENECK, 1983). As algas calcárias evoluíram ao longo do tempo geológico e tornaram-se abundantes durante o Pensilvaniano (*c.* 323 Ma; STENECK, 1983) mas somente a partir do Jurássico (*c.* 201 Ma) que este grupo se tornou mais abundante e diversificado nos recifes. Entretanto, foi a partir da radiação adaptativa iniciada no final do Cretáceo e continuada durante a era Cenozóica (*c.* 66 Ma; STENECK, 1983) que algas calcárias atingiram o período mais diverso da sua história evolutiva. Em relação ao seu papel na estruturação de recifes, do final do Carbonífero até o início do Permiano (*c.* 298 Ma), as algas calcárias mostraram-se importantes na construção destes ambientes, não por formar uma estrutura rígida, mas sim por aprisionar sedimento entre os ramos (WRAY, 1977; KIESSLING, 2009). Mais recentemente, estes organismos se consolidaram como bioengenheiros cimentadores e estruturadores de formações chaves para a manutenção da biodiversidade marinho-costeira em todos os oceanos do planeta.

Os recifes de algas calcárias não articuladas e corais como vemos atualmente surgiram no Cretáceo Superior (*c.* 80 Ma) e após se recuperarem da extinção em massa do fim do Cretáceo (*c.* 65 Ma, KIESSLING, 2008) diversificaram no início da Era Cenozóica e então declinaram no final do Paleoceno (*c.* 56 Ma; KIESSLING; FLÜGEL; GOLONKA, 2002) e por todo Eoceno (*c.* 56 Ma; KIESSLING, 2008, resumo Figura 2). Contudo, os ancestrais do grupo estão relacionados com o surgimento e diversificação dos herbívoros ao longo do Fanerozóico (*c.* 542 Ma) em função da sua capacidade de remover competidores por luz e nutrientes, como as epífitas, escavar o substrato calcário, predar e dispersar seus estruturadores (STENECK, 1983; BELLWOOD, 2003). Ainda, características morfoanatômicas e elevada capacidade de regeneração, como a deposição de carbonato de cálcio na parede celular, o escamamento de células do epitalo e peritalo, além do desenvolvimento da meristoderme, permitiram que as algas calcárias fossem menos vulneráveis à predação. Sua estrutura anatômica, caracterizada por ligações celulares, como conexões e fusões, possibilitaram uma eficiente translocação de recursos (nutrientes e gases) pelo hipotalo, mesmo quando regiões fotossinteticamente importantes eram danificadas (STENECK, 1983; PITLIK; PAUL, 1997).

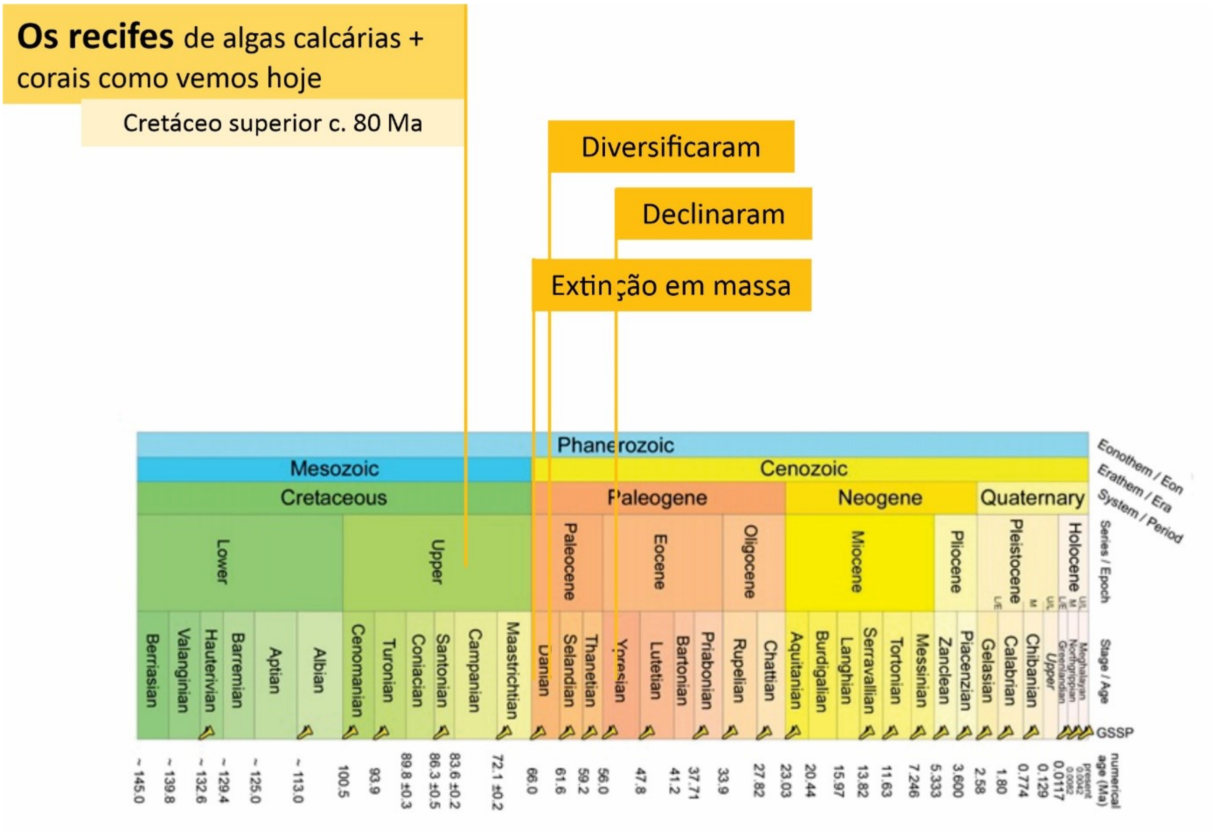

Figura 2. Resumo da história geológica dos recifes de corais e algas calcárias como conhecemos hoje, cuja origem remora o Cretáceo superior, já cerca de 80 milhões de anos atrás (adaptado de COHEN et al., 2013).

Os recifes do Atlântico Sul vêm se desenvolvendo desde o Cretáceo (*c.* 145 Ma), quando os continentes ainda estavam unidos em um mega bloco paleocontinetal, chamado Gondwana (PITTMAN et al., 1993). Com o início da separação deste mega continente, os oceanos Atlântico Sul e Central começaram a se formar, bem como a separação das placas Americana e Africana, há aproximadamente 100 Ma (MÜLLER et al., 2016), novas conexões assim como novas barreiras biogeográficas começaram a surgir. A nova conformação das placas tectônicas permitiu a colonização de espécies do Indo-Pacífico e do Atlântico Central, mas também do Pacífico Leste, passando pelo Istmo do Panamá, aberto até há aproximadamente 3,1–3,5 Ma (COATES; OBANDO, 1996; FLOETER; SOARES-GOMES; HAJDU, 2009). O fechamento final do Mar de Tethys há aproximadamente 12–19 Ma também foi um evento importante que impôs uma nova barreira física à conectividade entre o oceano Atlântico e Indo-Pacífico (STEININGER; RÖGL, 1984). Além dessas novas massas de terra que impuseram um bloqueio à passagem, outro aspecto importante a ser considerado no processo de formação dos recifes e, por consequência, na origem dos organismos recifais, são as barreiras 'suaves", conhecidas como filtros ecofisiológicos. Os filtros ecofisiológicos são processos oceanográficos, como, por exemplo, correntes de massas de água, longas distâncias preenchidas por mares profundos que, apesar de transponíveis, impõem obstáculos à dispersão dos organismos (FLOETER et al., 2008; LUIZ et al., 2012; COWMAN; BELLWOOD, 2013). Dentre eles, podemos mencionar a formação do mar profundo no Atlântico (*c.* 60 Ma, PITTMAN et al., 1993), o grande aporte de água doce proveniente do Rio Amazonas (barreira Amazônica, *c.* 6–10 Ma, HOORN et al., 1995) e a formação da Corrente de Benguela (*c.* 2 Ma, SHANNON, 1985; MARLOW et al., 2000). Considerando esses cenários, muitas hipóteses surgiram sobre a origem da flora marinha brasileira (OLIVEIRA, 1977; HORTA et al., 2001) a partir de aspectos da diversidade, processos geológicos e/ou oceanográficos (TAYLOR, 1955; JOLY, 1964; 1965; OLIVEIRA, 1977; HORTA et al., 2001).

Taylor (1955) considerou o Caribe um grande centro de dispersão no Atlântico Tropical devido a sua alta riqueza de espécies e endemismo. Por outro lado, Joly (1964; 1965), com base em aspectos oceanográficos atuais, propôs a flora marinha brasileira como centro de dispersão para o Caribe via corrente das Guianas. No entanto, Oliveira (1977) considerou que locais geologicamente mais antigos e ricos em espécies seriam centros de dispersão, portanto, o Caribe seria uma fonte de espécies para o Atlântico Sul. A partir de um banco de dados expandido e com base em análises multivariadas, Horta et al. (2001) trouxeram os processos oceanográficos históricos, ao se considerar a teoria da deriva continental e a formação do Atlântico Sul. Esses autores sugeriram que a flora Brasileira teve sua origem por diferentes rotas e momentos. A porção sul do Atlântico, ao sul da última conexão entre África e América do Sul, teria tido sua colonização original derivada do hoje Indo-Pacífico, enquanto a porção ao norte, representada pelos estados ao oeste do Rio Grande do Norte, colonizada por representantes caribenhos. Esses autores teorizaram ainda que mesmo com a separação total da América da África, há aproximadamente 100 Ma, as correntes que banhavam a costa brasileira não eram predominantes do Atlântico Norte, mas derivavam do hemisfério Sul para o Norte, com influências da circulação do oceano Índico, potencialmente trazendo propágulos e esporos que colonizaram a costa da África do Sul e a costa americana no Atlântico Sul (BERGGREN, 1980; HORTA et al., 2001).

A influência da tectônica de placas assim como a abordagem de centros de origem e dispersão têm sido recorrentemente discutidos em estudos biogeográficos (ROBERTSON et al., 2006; FLOETER et al., 2008; ROCHA et al., 2008; COWMAN; BELLWOOD, 2013; SIQUEIRA et al., 2019). De maneira geral, os padrões atuais de distribuição das espécies têm sido explorados por duas perspectivas, processos ecológicos e processos históricos (CRISCI, 2001; WIENS; DONOGHUE, 2004). Nos organismos recifais, a temperatura, tipo e disponibilidade de habitat têm sido historicamente as principais explicações ecológicas para os padrões observados (FLOETER et al., 2001; SANTOS et al., 2006; PEÑA et al., 2015; PINHEIRO et al., 2018). Ao passo que a capacidade de dispersão e presença de barreiras e/ou filtros ecofisiológicos vêm sendo apontados como importantes mecanismos de diversificação no ambiente marinho (FLOETER et al., 2008; MIGLIETTA et al., 2011; LUIZ et al., 2012)

O entendimento dos padrões atuais de distribuição das algas calcárias, assim como a história biogeográfica do grupo, nos permite refletir e teorizar sobre como esses organismos fotossintetizantes responderão às emergentes e intensas modificações dos ecossistemas marinhos e se coloca como um passo importante para o delineamento de estratégias de conservação destes organismos e de seus ecossistemas (RINDI et al., 2019).

As algas calcárias, assim como muitos outros organismos marinhos, estão sendo afetados pelas mudanças climáticas globais e acidificação dos oceanos (MARTIN; GATTUSO, 2009; MARTIN; HALL-SPENCER, 2017), além de ameaças regionais e locais, como o aporte de esgoto não tratado no ambiente marinho (SCHUBERT et al., 2019), desmatamento, escoamento de produtos químicos utilizados na produção agrícola, mineração marinha, vazamento de óleo (SISSINI et al., 2020), pesca predatória (STELLER et al., 2003). Estas atividades colocam em risco a saúde e os serviços ecossistêmicos prestados por esses organismos, que apesar de serem fundamentais precisam ser detalhados e melhor divulgados para que o *status* ou importância de sua conservação sejam de fato alcançados (HALPERN et al., 2019; MAGRIS et al., 2020).

Nas últimas duas décadas, os esforços em descrever a biodiversidade das algas calcárias no litoral brasileiro foram grandes (TÂMEGA; FIGUEIREDO, 2005; 2007; VILLAS-BÔAS et al., 2009; BAHIA et al., 2014a; BAHIA et al., 2014b; BAHIA et al., 2014c; SISSINI et al., 2014; BAHIA et al., 2015; COSTA et al., 2014; TÂMEGA et al., 2014; HENRIQUES et al., 2014a; HENRIQUES et al., 2014b; VIEIRA-PINTO et al., 2014; VILLAS-BÔAS et al., 2014; TORRANO-SILVA et al., 2014; BORGES et al., 2014; TÂMEGA et al., 2015; VILLAS-BÔAS et al., 2015; JESIONEK et al., 2016; TORRANO-SILVA et al., 2018; COSTA et al., 2019; JESIONEK et al., 2020), cujo enfoque foi principalmente na taxonomia e sistemática do grupo. Aspectos macroecológicos e evolutivos das espécies de algas calcárias no ASO ainda são pouco compreendidos.

As algas calcárias mostram-se um excelente modelo para estudos biogeográficos e evolutivos pois: **i.** estão amplamente distribuídas em todos os oceanos (FOSTER, 2001), desde regiões tropicais até regiões polares e encontram-se da zona entre marés até 268 m de profundidade (LITTLER et al., 1986) e ocorrem, inclusive, em sistemas aquáticos terrestres

(ŽULJEVIĆ et al., 2016); **ii.** compreendem o terceiro grupo mais diverso entre as rodófitas dos mares atuais, com aproximadamente 750 morfo-espécies reconhecidas (GUIRY; GUIRY, 2021); **iii.** caracterizam-se por depositar carbonatos na forma de calcita em suas paredes celulares (CABIOCH; GIRAUD, 1986; ADEY, 1998), garantindo uma boa preservação no registro fóssil o que possibilita inferir eventos de ramificação em uma árvore filogenética com robustez (AGUIRRE; PERFECTTI; BRAGA, 2010); **iv.** são organismos antigos, cuja origem já foi estimada para o início do Cambriano (YANG et al., 2016), tendo sido expostos às diversas pressões seletivas em uma ampla escala de tempo (PEÑA et al., 2020).

É inquestionável a importância ecológica das algas calcárias e o seu papel nos recifes do ASO. Os recifes biogênicos construídos por elas, com destaque para os bancos de rodolitos, constituem habitats estruturalmente complexos que abrigam assembléias de diversos grupos de animais (SIMON et al., 2016; CARVALHO et al., 2020b; VERAS et al., 2020; MOURA et al., 2021) e plantas marinhas (AMADO-FILHO et al., 2010, BRASILEIRO et al., 2016; CARVALHO et al., 2020a). Além disso, as algas calcárias são um dos organismos pioneiros no estabelecimento da comunidade, proporcionando substrato e os necessários atratores para o estabelecimento de outras macroalgas bem como o assentamento de larvas de invertebrados (FIGUEIREDO et al., 2007; GOLBUU; RICHMOND, 2007; SPOTORNO-OLIVEIRA et al., 2015). Em uma escala espacial menor, rodolitos funcionam como bancos de sementes de recifes por abrigar estágios microscópicos e diferentes fases do ciclo de vida de algas e invertebrados (FREDERICQ et al., 2019) e, então, facilitando processos de sucessão ou recuperação destes ambientes.

O presente estudo está organizado em três capítulos, os quais apresentam a biodiversidade das algas calcárias para o ASO (**Capítulo 1**), assim como os aspectos relacionados aos padrões atuais de distribuição das espécies das algas calcárias sob a perspectiva ecológica (**Capítulo 1**) e histórica (**Capítulo 2**). Os resultados encontrados nos **Capítulos 1** e **2** revelaram importantes parâmetros para o monitoramento e estratégias de conservação dos recifes costeiros, oceânicos e mesofóticos. Desta maneira, no **Capítulo 3**, foi apresentada, na forma de uma carta, a necessidade e urgência em se proteger as algas calcárias e os ambientes por ela formados.

1.1 OBJETIVO GERAL

Esta Tese tem como objetivo apresentar a biodiversidade de algas calcárias nos recifes brasileiros e avaliar como os processos e forçantes ecológicas e evolutivas estão relacionados aos padrões atuais de distribuição das algas calcárias não articuladas no ASO.

1.2 OBJETIVOS ESPECÍFICOS

Capítulo 1: este capítulo teve como objetivo quantificar a biodiversidade das algas calcárias no ASO e identificar as principais variáveis ambientais responsáveis pelos padrões de distribuição dentro e entre as ecorregiões, tendo como objetivos específicos:

- quantificar a riqueza de espécies das algas calcárias no ASO através de métodos de delimitação de espécies baseados em sequências de DNA;
- verificar a existência de padrão latitudinal na distribuição das espécies de algas calcárias através dos dados de riqueza de espécies e β-diversidade;
- identificar como as variáveis ambientais podem explicar as similaridades ou diferenças entre as principais ecorregiões do ASO;
- identificar, a partir dos resultados encontrados nos itens acima, áreas e ambientes prioritários para conservação.

Este capítulo foi submetido ao periódico *Coral Reefs* e encontra-se em revisão.

Capítulo 2: este capítulo teve como objetivo compreender a origem das espécies de Sporolithales que atualmente ocorrem nos recifes brasileiros a partir de uma perspectiva histórica. Os objetivos específicos deste capítulo são:

- quantificar a riqueza global atual de espécies de Sporolithales a partir de métodos de delimitação de espécies baseados em sequências de DNA;
- construir a filogenia global de Sporolithales baseada no marcador molecular *psb*A;
- verificar o padrão global atual de distribuição das Sporolithales em duas categorias geográficas: domínios e províncias;
- calibrar a filogenia a partir de modelos de relógio relaxado usando taxas não-correlacionadas com distribuição log-normal;
- estimar o estado ancestral dos principais clados de Sporolithales a partir de análises de máxima parcimônia.

Este capítulo será submetido ao periódico *Phycologia*.

Capítulo 3: este capítulo teve como objetivo apresentar a necessidade e urgência em se proteger as algas calcárias e os ambientes por ela formados diante do evento de vazamento de óleo no litoral brasileiro em 2018-2019.

Este capítulo foi publicado na revista *Science* em janeiro de 2020.

CAPÍTULO 1

DIVERSITY, DISTRIBUTION AND ENVIRONMENTAL DRIVERS OF CORALLINE RED ALGAE – THE MAJOR REEF BUILDERS IN THE SOUTHWESTERN ATLANTIC

(manuscrito em revisão no periódico *Coral Reefs*)

formatação de acordo com as regras da revista

2. CAPÍTULO 1: DIVERSITY, DISTRIBUTION AND ENVIRONMENTAL DRIVERS OF CORALLINE RED ALGAE – THE MAJOR REEF BUILDERS IN THE SOUTHWESTERN ATLANTIC

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ABSTRACT

Coralline red algae (CRA) are key players in the construction and maintenance of biogenic reefs and, they have important functional roles in ecological systems in the Southwestern Atlantic (SWA). Like many other marine organisms, CRA are currently affected by global and local stressors, but little is known about their biodiversity and the environmental drivers that influence their distribution patterns in the SWA. In the present study, we quantified the species richness of CRA in six ecoregions within the SWA using DNA-based species delimitation methods. We then verified their distribution and identified the main drivers shaping the macroecological patterns of richness and β-diversity. We found 79 phylogenetic species, that belong to the three main CRA orders (Sporolithales, Corallinales and Hapalidiales), in the tropical and warm temperate SWA. Temperature, nutrients, and water current velocity were the main environmental drivers of CRAs in the evaluated ecoregions. The Eastern Brazil ecoregion stands out due to its high richness, exclusive species, β-diversity between ecoregions and as a transitional zone of the SWA. The findings of our study have several important practical implications subsidizing actions for monitoring and conservation plans of coastal, oceanic and mesophotic zone, as the particularities of each ecoregion, the importance of the mesophotic habitat in owing unique species, as well as in connectivity with shallow habitats, and the ecological and evolutionary importance of the Transition Zone.

Keywords: Corallinophycidae, ecoregions, *psb*A, species delimitation methods

2.1 INTRODUCTION

Biogenic reefs are among the most diverse and threatened biological formations on the planet, providing high-value ecosystem services and functions still underestimated for coastal regions (Paoli et al. 2016). Worldwide, reef richness losses have been identified, quantified and monitored with coral-algal phase shifts found everywhere, a phenomenon where biogenic reefs shift from high levels of coral cover to persistent seaweed cover (Bellwood et al. 2004). Changes in reefs have been discussed considering systems where corals are the main builders, as in the Great Barrier Reef (Diaz-Pulido et al. 2009; Cheal et al. 2010) and in the Caribbean (Mumby 2009; Vermeij et al. 2010) while biogenic algal reefs have received little attention.

The tropical and warm temperate Southwestern Atlantic (SWA) spans a broad range of latitudes, including reef formations (Leão et al. 2003), in which coralline red algae (CRA) have shown to be key players in the construction and maintenance of these benthic ecosystems, but also due its abundance and functional role (Horta et al. 2016). These crustose calcifiers are ubiquitous in rochy shores and can build from fringe reefs to atolls. As other macroalgae or corals, also can have free living forms known as rhodoliths. Among the biogenic formations, rhodolith beds, a type of close cluster reef, following Riding's (2002) classification, deserve major attention. Carvalho et al. (2019) estimated that these free-living CRA may occupy up to 230,000 km^2 of the Brazilian shelf, from the Amazon's mouth (4º N, Moura et al. 2016) to the southern Brazil (27º S, Pascelli et al. 2013). By comparison, the Great Barrier Reef occupies 348.700 km^2. CRA are important components of all benthic reef communities evaluated along the Brazilian coast (Aued et al. 2018), often representing more than 30% of the benthic cover. CRA are also the main builders of the only atoll in the SWA, Rocas, where the abundance of CRAs varies between 36 to 72% in the reef composition (Gherardi and Bosence 2001).

Biogenic algal reefs constitute 3D complex habitats which accommodate diverse faunal (Veras et al. 2020) and floral assemblages (Amado-Filho et al. 2010). As community pioneers (Twist et al. 2019), CRA influence the settlement of fleshy algae and several species of invertebrates (Spotorno-Oliveira et al. 2015). Rhodolith beds serves as recruitment site for juveniles of several reef fish species (Pinheiro et al. 2014; Simon et al. 2016; Carvalho et al. 2020). Rhodoliths may also serve as 'seed' banks for microscopic stages of algae and invertebrates life cycles (Fredericq et al. 2019) and, thus, facilitate reef succesion or recovery.

Like many other marine organisms, coralline algae are currently threatened by global rises in temperature, ocean acidification and other chemistry changes (Caldeira and Wickett 2005; Zeebe et al. 2008). Meta-analyses have suggested that, while calcification rates of CRA may be more resistant to ocean acidification and warming than corals, for example, their photosynthetic rate and abundance are likely to be more susceptible (Kroeker et al. 2013). Local stressors, such as increased discharge of nutrients from sewage or fertilizers (Schubert et al. 2019), heavy metals from mining (Costa et al. 2019a), oil spills (Sissini et al. 2020), mining for calcite granulates (Pinheiro et al. 2019), dump of port dredging substrate (Pinheiro et al. 2019) and destructive fishing (*e.g.*, trawling, Foster 2001; Barbera et al. 2003) may contribute to further exacerbate global impacts on CRA, impacting negatively the net photosynthetic performance, calcification (Schubert et al. 2019) and consequently its growth and their ecosystem services.

In face of all these threats, a baseline on CRA biodiversity and distribution is essential for monitoring, managing, and conserving these widespread ecosystems. Furthermore, knowledge on CRA biodiversity patterns may offer insights on threats to ecosystem functioning (García and Martínez 2012), services and products (Loreau et al. 2001) mediated by these organisms.

Currently, 56 species of crustose and 17 articulated forms of the subclass Corallinophycidae, which includes four CRA orders, are recorded from Brazil with 30 recorded or described only in the last 10 years (Table S1). CRA taxonomy is notoriously difficult due to their densely calcified cell walls, with most of characters used to identify corallines before the molecular systematics era were revealed not phylogenetically significant. Taxonomic studies using molecular tools has shown the existence of cryptic or pseudo-cryptic species (Sissini et al. 2014; Gabrielson et al. 2018). Moreover, molecular systematics has greatly enhanced our ability to quantify CRA biodiversity, revolutionising their classification, and revealing many new species (Vieira-Pinto et al. 2014; Gabrielson et al. 2018; Torrano-Silva et al. 2018; Costa et al. 2019b; Twist et al. 2019; Jesionek et al. 2020; Peña et al. 2020).

Despite its unquestionable ecological importance and its critical role for SWA reefs, the patterns of distribution and species richness of CRA in this region are still largely unknown. Thus, the first aim of our study was to quantify the richness of CRA along the SWA Ocean, using DNA-based species delimiting methods and verifying the existence of a latitudinal gradient of CRA richness. We also aim to identify the main environmental drivers of these distribution and richness patterns. In particular, we expect that temperature and photosynthetically active radiation (PAR) will be key drivers of CRA richness and distribution due to their importance in mediating physiological and evolutionary processes (Keith et al. 2014; Gouvêa et al. 2017). Our analyzes will clarify how the environmental factors determine biogeographic patterns of CRA and whether these patterns recover the divisions in ecoregions proposed by Spalding et al. (2007) or the scenario of a large tropical-Caribbean province, as observed for other marine organisms (Floeter et al. 2018; Pinheiro et al.2018). The clarification of the richness of CRA, β-diversity can subside conservation strategies recognizing areas of greater biodiversity, as well as important regions due to high connectivity.

2.2 MATERIAL AND METHODS

2.2.1 Study area

The Southwestern Atlantic Ocean presents a mosaic of oceanographic conditions. Its waters are mainly influenced by the Brazil Current (BC), which originates from the bifurcation of the Equatorial South Current (ESC), south of 10ºS, and flows south, bordering the South American continent to the region of the Subtropical Convergence (38± 2ºS, Olson et al. 1988), where it forms the confluence with the Malvinas Current (MC) and moves away from the coast. The other section of the ESC goes north, forming the North Brazil Current (NBC). While the BC is characterized by warm and oligotrophic waters, the MC is dominated by cold and nutrient-rich waters (Piola et al. 2018). Another important influence in the warm temperate region of Brazil, is the intermittent arrival of the plume of the Plata River (Pimenta et al. 2005; Piola et al. 2018). These cold and nutrient-rich waters, with relatively low salinity widely influences coastal ecosystems up to latitude 23ºS (Pimenta et al. 2005).

The continental shelf varies substantially in width along the coast, having its maximum width near the Amazon mouth (app. 330 km), and becoming narrower along the northeastern and eastern shelves, before enlarging again in the south towards the Plate River (Martins and Coutinho 1981).

Reefs are distributed along four geographic regions: northern, northeastern, eastern and southern, being predominantly biogenic from northern to eastern and replaced by rocky reefs from the south of Espírito Santo (20ºS) to the north of Rio Grande do Sul (29ºS, Leão et al. 2003). On the other hand, rhodolith beds are observed throughout the whole Bazilian shelf, from the northern tropical to the southern warm temperate edge (Carvalho et al. 2020).

2.2.2 Database

A research network was established with the main experts on coralline red algae in Brazil who contributed with unpublished data and ongoing PhD theses information. Additionally, an exhaustive literature review was carried out. Only occurrences with DNA sequences were considered, since the identification of species based only on morphology can prove to be inaccurate and flawed (as previously elucidated in the introduction), so we used the concept of Molecular Operational Taxonomic Unit (MOTU, Floyd et al. 2002) as the basis for species delimitation. As the gene that codes the D1 protein of the thylakoid membrane of photosystem II (*psb*A) was the most commonly used marker among studies carried out with specimens from Brazil, we filtered the occurrences by this marker. Furthermore, *psb*A has been showing enough interspecific variation for species delimitation and has been used for the identification of new species among Corallinophycidae, such as *Lithophylllum atlanticum* Vieira-Pinto, Oliveira et Horta (Vieira-Pinto et al. 2014) and *Sporolithon tenue* Bahia, Amado-Filho, Maneveldt et Adey (Bahia et al. 2014). All representatives of Corallinophycidae were included, geniculate and non-geniculate species and, encrusting and rhodolith forms from tidal pools, rocky shores, reef crests, atoll and rhodolith beds.

A total of 327 occurrences were compiled from 145 sites along the Brazilian coast, continental shelf and three oceanic islands (Fernando de Noronha Archipelago, Rocas Atoll and Trindade Island), which were divided by ecoregions, according to Spalding et al. (2007).

New collections, DNA sequencing and species delimitation and phylogenetic analyses are described in Supplementary Material (SM1-3).

2.2.3 Patterns of species turnover and nestedness

The patterns of species turnover and nestedness among ecoregions were evaluated based on presence and absence of species. Beta diversity was calculated through the Jaccard dissimilarity coefficient (β-diversity; β_{JAC}), which was then partitioned into components of dissimilarity due to turnover and nestedness. From the R package "betapart", the function "beta.multi" was used to calculate multiple-site dissimilarities, and the function "beta.pair" was used to calculate pairwise measurements of Jaccard dissimilarity (Baselga and Orme 2012).

2.2.4 Relating coralline algae richness to environmental variables

Prior to analysis, occurrences of CRA were presence-absence transformed based on species delimitation methods described in section *2.5*. For the evaluation of environmental drivers, we constrained our dataset to records from 10m depth or shallower, a total of 305 records (93% of the total database)

The differences between the ecoregions with respect to CRA richness were examined using PERMANOVA, based on Sorensen's similarity using 999 permutations (Anderson 2001).

We initially considered 12 environmental variables (Table S3, Tyberghein et al. 2012; Assis et al. 2018) as potential predictors of coralline red algae richness based on Carvalho et al. (2019). However, these variables were highly correlated, and a selection of variables was necessary. It was selected seven variables by the DistLM analysis: maximum and minimum current velocity, maximum and minimum phosphate concentration, minimum salinity, maximum and minimum ocean temperature. Environmental data obtained from BioOracle (www.bio-oracle.org, Tyberghein et al. 2012; Assis et al. 2018) were Logx+1 transformed and normalized prior to the calculation of similarities in order to down weight the importance of differences in scale of the parameters evaluated. To determine which environmental factors showed the highest correlation to the biological resemblance matrix similarity patterns, data were analysed by Distance-based Linear Model (DistLM, Anderson 2001). DistLM routine provides an insight into the correlation between environmental parameters and the biotic community by comparing all combinations of environmental data with the biotic assemblage by Spearman rank correlation. It determines an 'optimum' or the best possible combination of environmental variable which provides greatest correlation with the biological data. SIMPER analysis was conducted to identify which environmental variables contributed most to Euclidean distance between ecoregions (Clarke 1993).

Patterns of coralline algae richness distribution and its relationship with the environmental drivers were explored using a redundancy analysis (dbRDA). All the statistical analyses were performed using R software v.3.5.0 (R Core Development Team 2018) and Primer v.6.1.13 with Permanova v.1.0.3 extension.

2.2.5 Data deposition

Data available from the Ocean Biodiversity Information System (OBIS - IODE - IOC/UNESCO): http://ipt.iobis.org/wsaobis/. DNA sequences were deposited in GenBank (https://www.ncbi.nlm.nih.gov/genbank/).

2.3 RESULTS

2.3.1 Phylogenetic results

In this study, we generated 192 new sequences, which, combined with previously sequenced samples, revealed 79 phylogenetic species of Corallinophycidae to the SWA tropical and warm temperate region (Figs. 2 and S1–3). The Eastern Brazil ecoregion (#5 in Fig.1) was the richest (Table 1), with 50 recorded MOTU, followed by Southeastern Brazil (27 MOTU, #7 in Fig.1,) and Northeastern Brazil (23 MOTU, #4 in Fig.1). Twenty-one MOTU from Eastern Brazil have only been collected in this ecoregion. Regarding species occurring in the mesophotic zones, three MOTU are exclusive to deep waters (MOTU46, MOTU16, MOTU12), five MOTU are shared between shallow and deep habitats (MOTU 24, MOTU19, MOTU17, MOTU05, MOTU1), and we found one singleton (MOTU 62).

Sporolithales - Eight taxa were delimited in the Sporolithales, of which at least four were morphologically identified as *Sporolithon* (MOTU 19 as *S. yoneshigueae* in Bahia et al. 2015; MOTU 24 as *S. amadoi* in Richards et al. 2019; MOTU 25 as *S. tenue* in Bahia et al. 2014 and MOTU 62 as *Sporolithon* sp. in Jesionek et al. 2016). All taxa belong to the tropical province, occurring in Trindade and Martin Vaz, Fernando de Noronha and Rocas Atoll oceanic islands, Northeastern and Eastern Brazil ecoregions. MOTU 19, MOTU 24 and MOTU 62 have specimens occurring deeper than 50 m.

Corallinales - Our study identified 45 taxa of Corallinales (16 of them are articulated forms), belonging to at least 10 different genera: *Amphiroa, Harveylithon, Hydrolithon, Lithophyllum*, *Neogoniolithon, Paulsilvella, Pneophyllum, Porolithon, Titanoderma* and *Tomitolithon.* Representatives of this order are widely distributed in tropical and temperate provinces of Brazil. However, some taxa are exclusive to some ecoregions (*e.g*., MOTU 27 and 33 to Northeastern Brazil, MOTU 38 to Eastern Brazil) and others are widely distributed (*e.g*., MOTU 34 and 29). MOTU 16, morphoanatomically identified as *Lithophyllum*, was found only for deep habitats (94 to 101 m deep). Seventeen MOTU are represented by only a single sample (singleton) in our dataset.

Hapalidiales - This order presented 26 MOTU, with representatives widely distributed along the Brazilian coast, as *Melyvonnea erubescens* (MOTU 3), while others were restricted to the tropical province (MOTU 8, 10, 15). Still, MOTU 1, 12 and 16 were identified only for deep habitats (deeper than 50m). MOTU 5 and 17 were found from shallow to deep habitats. Among Hapalidiales, only *Melyvonnea erubescens*, *Crustaphytum atlanticum* and *Tectolithon fluminense* have already been morphologically described. Nine MOTU were represented by only one sample.

2.3.2 Patterns of species turnover and nestedness

Turnover ($\beta_{turnover} = 0.81569$) is the main component of β-diversity ($\beta_{JAC} = 0.91376$), explaining species variation between ecoregions. In the pairwise comparison of ecoregions (Fig. 3, Table S3), the highest values of turnover were observed between the geographically distant Amazonia and Trindade and Martin Vaz Islands and, Amazonia and Southeastern ($\beta_{turnover} = 1$). Meanwhile nestedness was greater among the neighboring ecoregions Fernando de Noronha and Rocas and Trindade and Martin Vaz Islands ($\beta_{nestedness} = 0.35185$), Northeastern and Amazonia ($\beta_{nestedness} = 0.30857$) and, Trindade and Martin Vaz Islands and Eastern Brazil ($\beta_{nestedness} = 0.21299$).

2.3.3 Coralline richness and environmental drivers

PERMANOVA showed that ecoregions have environmental particularities that cause significant richness changes. There was a difference between the biological variables of the Eastern and Southeastern ecoregions ($p = 0.001$), Eastern and Northeastern Brazil ($p = 0.001$) and Southeastern and Northeastern Brazil ($p = 0.001$) (Table S5).

SIMPER analysis evidenced the environmental variables with greater relative importance explaining similarities within ecoregions, as shown in the Fig. S4.

When evaluating the environmental variables with the greatest contribution to the dissimilarity between ecoregions, we obtained different combinations for each ecoregion pair evaluated, as shown in Fig. S5.

The first two dbRDA axes, illustrate the interaction between biological and environmental variables, accounted for 8.46% of the total variation and 58.21% of the variation of the fitted model, while 14.54% of the total variation and 100% of the fitted model were explained by the 8 first axes (Table S6). Data dispersion were explained by a direct relationship of the first axis to long-term minimum ocean temperature ($R= 0.657$) and long-term maximum current velocity ($R= 0.437$) and while it is inversely related to long-term maximum phosphate concentration ($R= -0.445$). The second axis of the dbRDA was inversely related to long-term minimum salinity ($R = -0.764$) and long-term minimum current speed ($R = -0.389$) and directly related to long-term maximum current velocity ($R = 0.347$).

RDA still revealed high correlation of Southeastern Brazil sites with maximum phosphorus concentration, Northeast Brazil with maximum and minimum temperature and maximum current velocity and, Eastern with minimum salinity and minimum current velocity, as shown in Fig. 4.

2.4 DISCUSSION

In this study we revealed 79 phylogenetic species of CRA in the SWA reef systems. This number is over three times higher than the richness of known coral builder species (Leao 2016). Thus, our study not only emphasises the richness of CRAs in SWA reefs (Aued et al. 2018; Gherardi and Bosence 2001) but suggests that this group may not have faced the same evolutionary constraints as other groups of reef builders (*e.g.*, Scleractinian corals), at least not in the same magnitude.

Despite many species being described in the last decade, this is the first work that presents the richness of the whole group (Corallinophycidae) at a regional scale. The drivers that better correlate to each ecoregion and its CRA richness, β-diversity and distributional patterns are sea surface temperature, phosphate concentration and current velocity. Thus, our study supports findings of Carvalho et al. (2019) on the importance of these variables in defining niche suitability for species on this group. As higher irradiances tend to co-occur with higher temperatures, some of the effect of temperature on CRA may potentially be attributed to the quantity and quality of photosynthetic active radiation driving growth, survival and reproduction (Ichiki et al. 2006).

Our findings have several important practical implications. Firstly, they emphasise the importance of biogeographic transition zones in driving richness patterns, as observed to other groups, such as birds (Smith et al. 1997; Kark et al. 2007a), plants (Traut 2005), spiders (Traut 2005) and reef fishes (Pinheiro et al. 2018a), drawing attention to the importance of preserving different evolutionary responses to changes in climate and environment (Smith et al. 2001). Secondly, the distinct flora of deep waters deserves to be more studied and better preserved as they can represent a cooler refuge in future warmer conditions, at the same time connectivity to shallow environments, seen by sharing five MOTU. Last but not least, conservation initiatives should consider the peculiarities evidenced in the five ecoregions. Analysis to undertake a large-scale spatial prioritization of marine protect areas in the Brazilian platform show that priority should be given to several clumps considering places of high biodiversity, as well as those that represent greater connectivity between habitats, as mesophotic reefs and rhodolith beds (Magris et al. 2020).

CRA richness in the SWA

Approximately 40% (29 of 79) of the total species found comprised single specimens (singleton). In a recent study on CRA diversity in New Zealand (NZ), Twist et al. (2019) stressed the high representation of singletons (25%) and argued that more collections of these specimens are essential for understanding their ecology and distribution. Among other groups of organisms, such as arthropods and vertebrates, the percentage of new species discovered represented by a singleton is also high, 30% and 19%, respectively (Lim et al. 2012). Emphasizing the possibility of representing new species.

Our study revealed eight phylogenetic species for Sporolithales (of a total of 79), occurring only in tropical regions. In NZ, four species of *Sporolithon* were recorded in a survey that found 122 species. *Sporolithon* is the only genus among the Sporolithales recorded in

Brazil, with 10 species registered (Table S1). However, four species need revision (*S. australasicum*, *S. eryhraeum*, *S. howei* and *S. pacificum*) and only three species (*S. tenue*, *S. amadoi* and *S. yonehigueae*) were molecularly characterized. Sporolithales is relatively less diverse when compared to the other two orders of Corallinophycidae. Among living species, Sporolithales occurs in tropical shallow water and temperate seas (Ghosh and Sarkar 2013). In Brazil, Henriques et al. (2014) registered three species in mesophotic waters in the temperate zone.

Prior to this work, 30 crustose species (excluding articulated forms) of Corallinales were known for the SWA, with five species in need of taxonomic revision. Our study revealed 45 species and a high supported infrageneric resolution is due to previous studies that focused on the diversity of this order (Vieira-Pinto et al. 2014; Torrano-Silva et al. 2018; Costa et al. 2018b). Ecologically, Corallinales occupy different habitats in the SWA reefs, as a framework in biogenic reefs (*e.g.*, *Porolithon* in Rocas Atoll, Gherardi and Bosence 2001), are important and abundant in rock reefs (*Lithophyllum atlanticum* in Southeastern Brazil, personal observation) and in rhodolith beds (Pascelli et al. 2013). It also worth highlighting the role of articulated forms in the composition of calcareous turf and as free-living forms (articuliths), unique to SWA (Tâmega et al. 2017).

Hapalidiales was the second most diverse order in our study (26 species), and which had a greater increase in the known diversity (previously 16 species had been registered). However, the great difficulty in the systematics and taxonomy of this group suggests there might be identification biases associated to this group. Studies using molecular markers have shown new genera and species and the potential underestimation of biodiversity (Sissini et al. 2014; Jesionek et al. 2020).

CRA distribution

Our results showed that the greatest CRA richness is found between latitudes 12º S to 22º S (Eastern Brazil n= 50 MOTU). Focusing on the genera richness of Rhodophyta on a global scale, Keith et al. (2014) identified a similar pattern to SWA.

The Eastern Brazil ecoregion has also been revealed as the richest for other marine organisms, such as reef fishes (Floeter et al. 2008; Pinheiro et al. 2018b) and prosobranch gastropods (Barroso et al. 2016). This ecoregion (#5 in Fig. 1) includes the state of Espírito Santo, considered a transition zone in terms of macroalgae diversity by Horta et al. (2001). The high richness and β-diversity nestedness values of marine macroalgae in this region is suggested by the wide variety of habitats (Kark et al. 2007b), including chemical composition and substrate rugosity (Mazzuco et al. 2020), and regional and seasonal current patterns (Stramma and England 1999).

Transition zones can be considered diversity hotspots, these ecotones present environmental conditions that allow the co-occurrence of species with different ecophysiological requirements and the co-occurrence of different haplotypes within the same population (Sissini et al. 2014; Ayres-Ostrock et al. 2019; Nauer et al. 2019). Furthermore, these transitional areas hold high levels of rare species (Kark et al. 2007), as observed in our study. Kark et al. (2007) have suggested that both evolutionary and ecological processes interact and are responsible for high richness and high rarity coincidence in transition zones.

2 Ecologically, the transition zone presents more than the combination of two environments, it presents particularities that allow to sustain unique species (Kark et al. 2007; Smith et al. 1997). Espírito Santo comprises the south edge of distribution of tropical CRA species in the SWA (*e.g.*, *Sporolithon* spp.), but also the north edge of the distribution of temperate species, such as *Neogoniolithon crypticum.* In addition, this region also contained 21 unique species.

We found that some species of CRA (MOTU 5 and 17) occurred both in shallow and deep waters (< -50 m), raising the importance of the connectivity of these environments for understanding the group origin and diversification. For stylasterid corals, phylogenetic studies have shown that deep-water corals have invaded shallow-water in the tropics three times, with one additional invasion of the shallow-water temperate zone (Lindner et al. 2008).

Even among the deep-water species, 3 of them (MOTU 1, 12 and 16) were not observed in shallow waters, suggesting that deep habitats present distinct environmental conditions and species composition. Graham et al. (2007) have shown potential areas suitable for kelps even in the tropics due to deep-water habitats that can offer favorable conditions to typically temperate species. In the face of climate change, these deep euphotic zone refugia have important implications for the maintenance of species, since deep areas can be dampened from disturbances that affect shallow waters (Assis et al. 2016).

We found that some MOTU are shared between adjacent ocean and coastal ecoregions, showing that there was/is somehow connectivity between the oceanic archipelago Trindade and Martin Vaz and Eastern Brazil (MOTU 3, 4 and 34). The Vitória-Trindade Chain is made up of a series of seamounts that start close to the coast and extend to these islands, which are their only emerged portions, acting as stepping stones between these two extremes, as already demonstrated for reef fish (Pinheiro et al. 2018).

Environmental drivers

Our study highlighted a combination of 7 different physical/chemical environmental drivers that explain, at different scales, the distribution patterns of CRA. The study area stretches across 29 degrees of latitude (from 1ºN to 27ºS), which naturally implies a wide variety of ecological conditions resulting from differences in abiotic variables (Adey and Steneck 2001) and biological interactions, such as herbivory – the major biotic driver of macroalgal composition (*e.g.*, Floeter et al. 2005; Bonaldo and Hay 2014; Longo et al. 2015).

Temperature is known to be an important factor driving species richness and community composition, influencing the occurrence (van den Hoek 1987), growth, phenology (de Bettignies et al. 2018) and metabolism (Allen et al. 2006) of species. Allen et al. (2006), for example, found that there is a positive correlation between the rates of DNA evolution and environmental temperature as well as the individual metabolic rate, warmer locations having higher speciation rates and consequently more species. In our study, the minimum sea surface temperature (SST) proved to be the main explanatory variable in the differences between the richness of CRA, with maximum values of minimum SST in Amazonia (27ºC, maximum SST 29ºC) and minimum in Southeastern Brazil (17ºC, maximum SST 26ºC). The transition zone has 21ºC (minimum SST) and 29ºC (maximum SST) reinforcing, from the perspective of this variable, to be an area of considerable overlap of environmental conditions allowing the occurrence of tropical and temperate species.

CRA seem to be very tolerant to low salinities, which is corroborated by the existence of rhodolith beds in areas adjacent to the mouth of the Amazon (21 psu, Moura et al. 2016) and even in freshwater, as *Pneophyllum cetinaesis* in the Cetina River (Croatia, Zuljevic et al. 2016). Laboratory experiments have shown that species systematically exposed to lower salinity conditions in nature due to summer thaw, such as *Lithothamnion glaciale*, do not show significant changes in their photosynthetic performance (Fv/Fm) when exposed to salinities of 40, 33 and 15 psu, remaining alive at salinities down to 3 psu (Wilson et al. 2004). On the other hand, *Phymatolithon calcareum* shows a decrease in its photosynthetic efficiency at a salinity of 15 psu (Wilson et al. 2004) suggesting a species-specific response to salinity and the role of this variable as an environmental filter for some species of CRA.

The current velocity had a great influence on the dissimilarities between the ecoregions, especially those characterized by oceanic environments (Fernando de Noronha and Rocas Atoll and Trindade and Martin Vaz Islands). Carvalho et al. (2019) have shown a negative correlation between the richness of marine macrophytes and hydrodynamics, corroborating the influence of this variable on the distribution of CRA. Hall-Spencer and Moore

(2000) have also stressed the importance of currents to the free-living CRA abundance. Movements to which rhodolith or maërl are susceptible remove epiphytes and associated fauna, reducing competition and favoring their acquisition of energy. On the other hand, low hydrodynamics favor sedimentation and consequent decreased light availability, compromising CRA settlement and photosynthesis (Riul et al. 2008).

Our results showed that the maximum phosphate concentration has an indirect relationship with biodiversity patterns in CRA. Low concentrations of nutrients can be limiting (Delgado and Lapointe 1994) nevertheless, nutrient, when in excess, can damage the macroalga metabolism (Bjork et al. 1995). Experimental conditions showed that phosphate has an inhibitory effect on both the growth and the calcification rate of CRA, due to phosphorus adsorption to carbonate particles (Delgado and Lapointe 1994). Another important aspect to note is that the high availability of nutrients can favor opportunistic species (fleshy algae), which have rapid growth and would make it difficult the establishment of CRA, which despite being more biologically adapted to the environment (Littler and Arnold 1982), have greater ecological success in environments with low nutrient availability, as observed in our study (Fig. S4).

Conservation Implications

Understanding the structuring forces that control the spatial variation in biodiversity has a practical role in predicting how species will respond to environmental changes and in structuring a robust conservation plan (Mellin et al. 2016; Quimbayo et al. 2019).

Habitat loss, degradation, fragmentation and pollution, overexploitation of marine resources and invasions of alien species, added to global climate changes are the main threats to CRA (Díaz et al. 2019; Rindi et al. 2019; Schubert et al. 2019). Considering their role as reef builders, not only species but also habitats are vulnerable (Weiss and Martindale 2017).

In Australia and Europe, coralline algal habitats are either protected from trawling and dredging impacts (Grall and Hall-Spencer 2003) or are within a Marine Protected Area (MPA) network. For example, in Spain, 28% of known rhodolith beds are located within MPAs and another 19 unprotected beds have been proposed for future conservation actions (Hernandez-Kantun et al. 2017). Still, maërl are among the priority marine environments for protection in the North-east Atlantic, in an international cooperation signed at OSPAR (Oslo Paris Convention). Brazil has its largest oil production fields located within the rhodolith beds (*e.g.*, Campos Basin), which puts these environments even at more risk. This can be typified by the

2019 spill of 4,000 tons of crude oil with largely unknown consequences to CRA (Soares et al. 2020).

Despite scientific recognition of the importance of rhodolith beds and their environmental services for the ongoing ecosystem health of coastal seas in many regions, these organisms are still unprotected, even after the recent increase of Marine Protected Areas coverage (Soares and Lucas 2018). The conservation status is set back in the SWA, *e.g.*, as the Brazilian government allowing the mining of CRA in the most biodiverse seamount of the Vitoria Trindade Chain.

CRA, highlighting the rhodolith beds, are a jewel in the crown of the world's marine heritage for their biodiversity, vast distribution, and great ecological and economic importance, and the findings of our study help Brazil and the United Nations to provide new arguments considering management of marine systems and to achieve the Development Goal (SDG) 14, providing new horizons into the Decade of Ocean Science for Sustainable Development.

Priority actions for monitoring and conservation plans should consider what our results showed: (i) the peculiarities in the biodiversity of CRA in each of the ecoregions; (ii) the role of the transition zone in concentrating biodiversity, both in tropical and temperate regions, representing a hotspot for CRA and a region of the utmost importance for conservation as a world heritage and; (iii) the importance of habitats in deep waters as maintainers of a unique biodiversity, as well as in its role as a refugia to marine flora from shallow waters.

2.5 ETHICAL DECLARATIONS

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2.5.2 Conflict of interest statement

On behalf of all authors, the corresponding author states that there is no conflict of interest.

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TABLES

Table 1. Number of Molecular Operational Taxonomic Units (MOTU) of coralline red algae recorded for ecoregions in the Southwestern Atlantic Ocean. Ecoregions were divided according to Spalding et al. (2007). (#) number of ecoregions in Fig 1.

(#) Ecoregion	No. MOTU
(1) Amazonia	5
(3) Fernando de Noronha and Rocas Atoll	12
(4) Northeastern Brazil	23
(5) Eastern Brazil	50
(6) Trindade and Martin Vaz Islands	9
(7) Southeastern Brazil	27

FIGURES

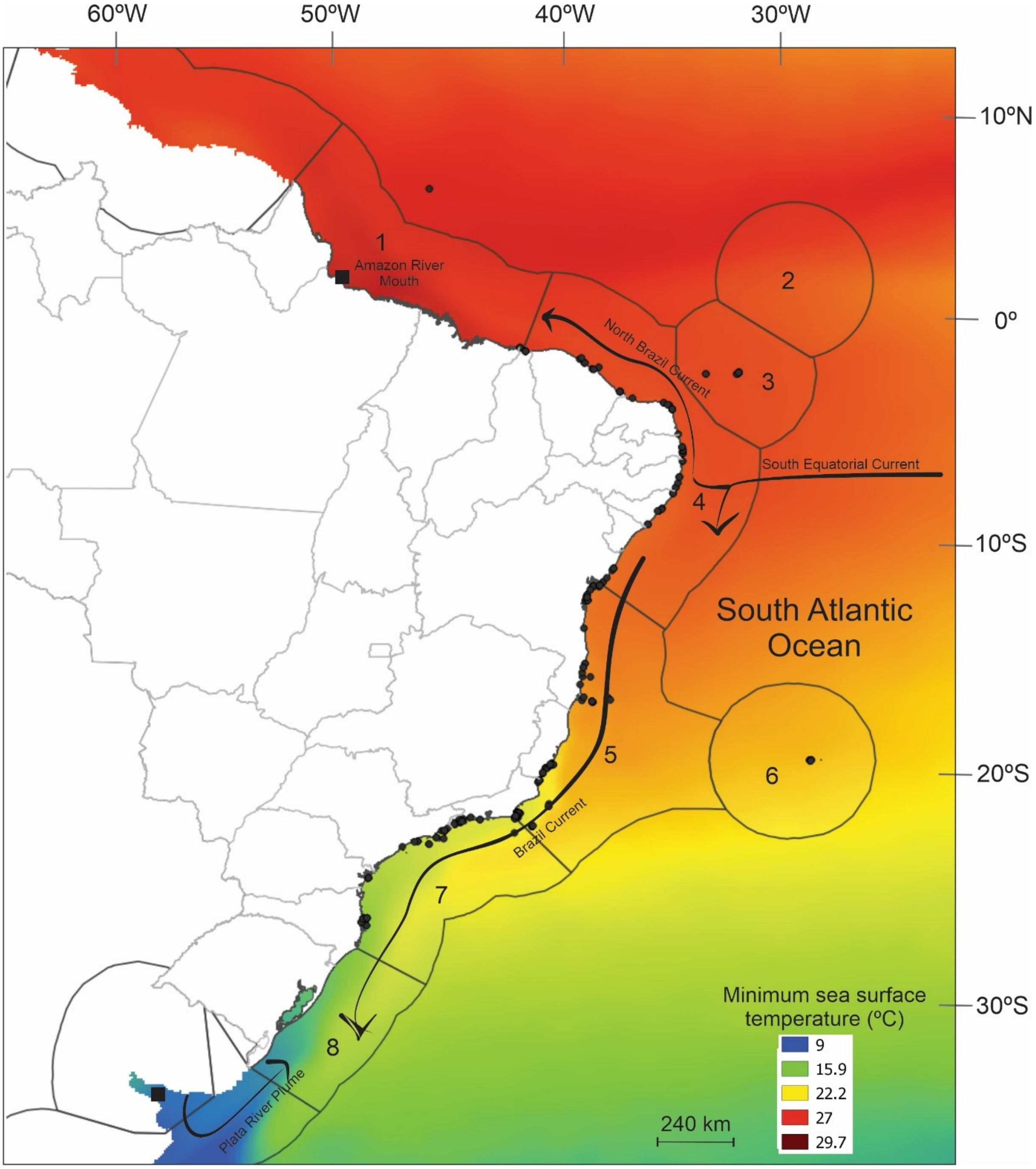

Fig. 1 Study area divided in ecoregions, following Spalding et al. (2007). Due to logistical difficulties imposed by the region, it was not possible to collect in Ecoregion 2 and in Ecoregion 8 there is no consolidated substrate for algae growth and rhodolith beds are unknown. Black dots represent collection sites (n=145) for which Corallinophycidae samples had *psb*A sequences. **North Brazil shelf**: (1) Amazonia; **Tropical south western Atlantic**: (2) S. Pedro and S. Paulo Archipelago, (3) Fernando de Noronha and Rocas Atoll, (4) Northeastern Brazil, (5) Eastern Brazil, (6) Trindade and Martin Vaz Islands; **Warm temperate south western Atlantic**: (7) Southeastern Brazil and, (8) Rio Grande. Colors represent the minimum average temperature of the ocean surface in the period from 2000 to 2014, data extracted from BioOracle (www.bio-oracle.org). Color legend is indicated in the lower right corner of the figure.

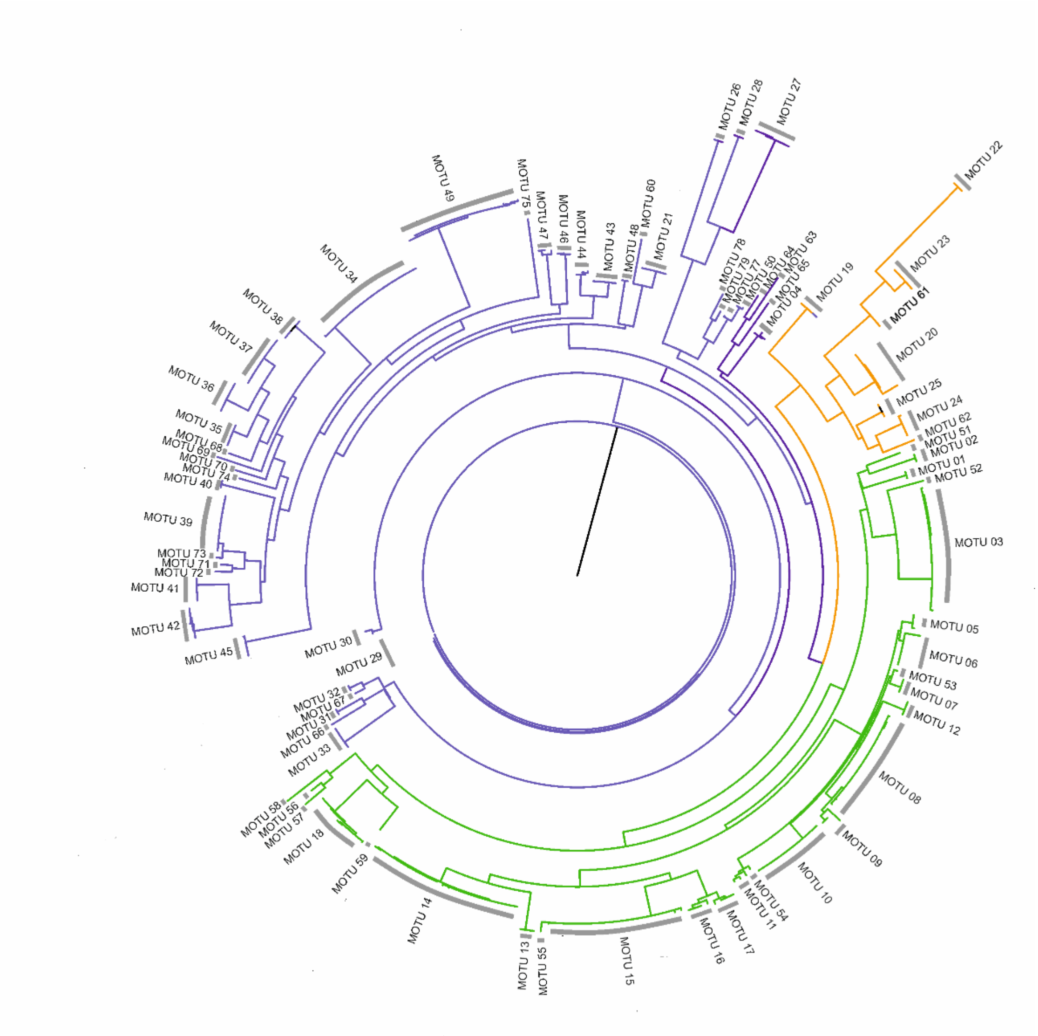

Fig. 2 Maximum likelihood *psb*A tree for Corallinophycidae in the Southwestern Atlantic Ocean (SWA). Gray bars represent the consensus between three methods of species delimitation: the single threshold Generalized Mixed Yule Coalescent (sGMYC), the Bayesian Poisson-Tree Processes (bPTP) and, Automatic Barcode Gap Discovery (ABGD). We considered the Molecular Operational Taxonomic Unit (MOTU, Floyd et al. 2002) as the unit for species. Tree nodes colors represent the three orders of Corallinophydae: orange Sporolithales, green Hapalidiales and purple Corallinales.

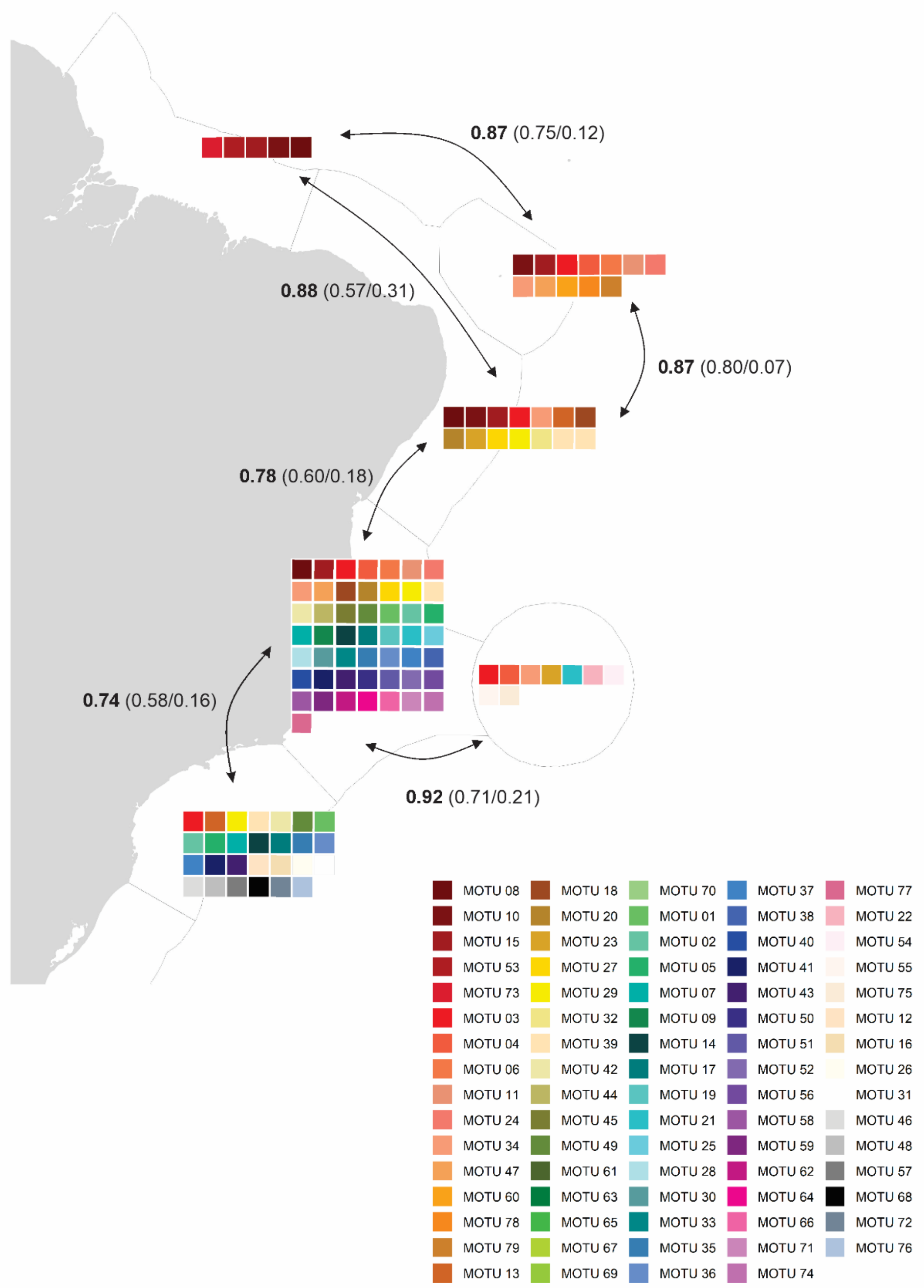

Fig. 3 Species richness of coralline red algae (CRA) and Jaccard beta diversity ($\beta_{JAC,}$ numbers in bold) along and between Ecoregions (according Spalding et al. 2007) in the Southwestern Atlantic Ocean (SWA). Each phylogenetic species, delimited through the *psb*A molecular marker, was defined as Molecular Operational Taxonomic Unit (MOTU), was represented by one square of a specific color. Jaccard beta diversity decoupled in its respective turnover ($\beta_{turnover}$, numbers in italic) and nestedness ($\beta_{nestedness}$, numbers in normal caps) components among SWA ecoregions.

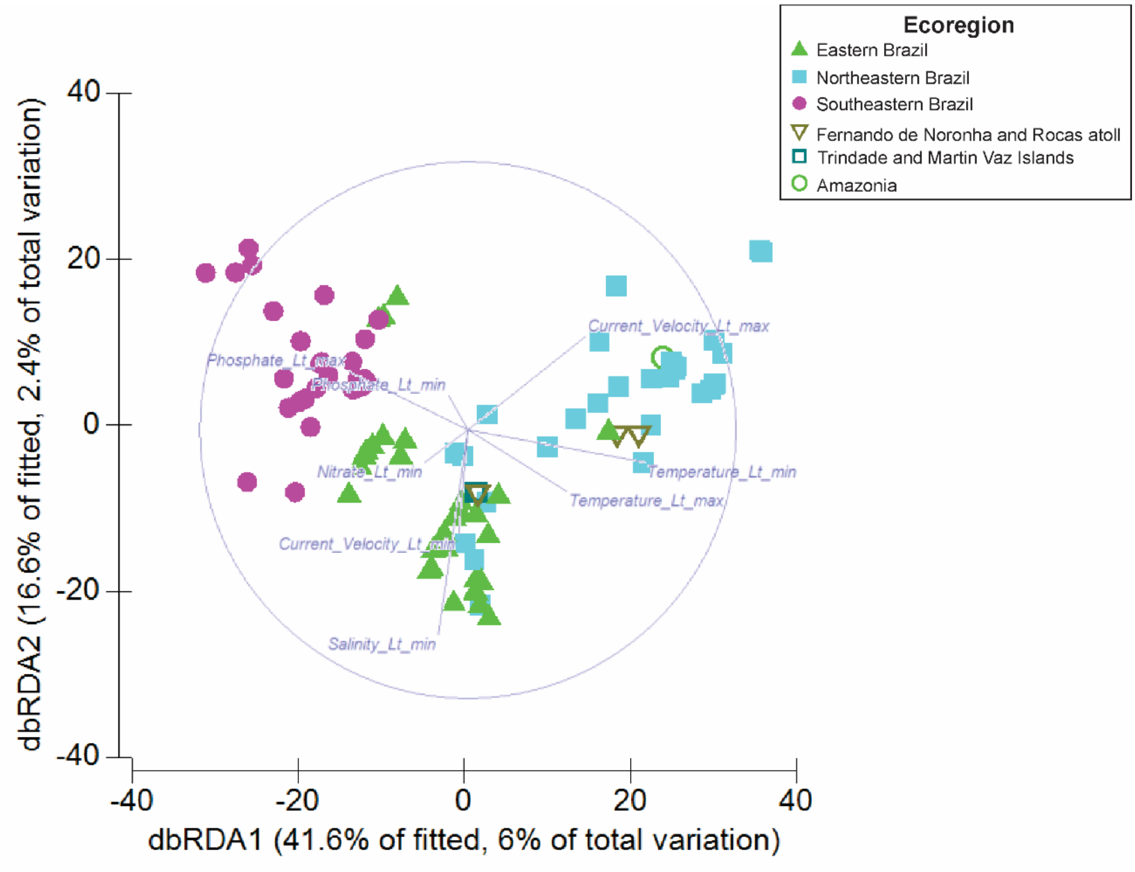

Fig. 4 Results of the distance-based multivariate multiple regression (DistLM) of CRA ocurrence data overlaid with the partial correlations of the significant environmental variables identified by the best models using the AICc criterion. The Redundancy Analysis (dbRDA) grouped the occurrences by ecoregions, represented by different symbols and colors. In both the first and second axes, data dispersion is explained by physical factors, directly related to long-term minimum ocean temperature (R= 0.657) and inversely related to long-term minimum salinity (R= -0.764), respectively.

SUPPLEMENTARY TABLES

Table S1: Current species of Corallinophycidae registered to Brazil and main references. § indicates the articulated forms * indicates species that have some region of DNA sequenced # indicates species that need review

	Important references to Brazil
SPOROLITHALES	
SPOROLITHACEAE	
Sporolithon australasicum (Foslie) Yamaguishi-Tomita ex Wynne#	Oliveira Filho (1977)
Sporolithon elevatum Henriques and Riosmena-Rodriguez	Henriques et al. (2014a)
Sporolithon episporum (Howe) Dawson	Oliveira Filho (1977), Nunes et al. (2008), Costa et al. (2014), Bahia et al. (2015)
Sporolithon erythraeum (Rothpletz) Kylin #	Oliveira Filho (1977)
Sporolithon howei (Lemoine) Yamaguishi-Tomita ex Wynne#	Oliveira Filho (1977)
Sporolithon molle (Heydrich) Heydrich	Bahia et al. (2014a)
Sporolithon pacificum Dawson#	Oliveira Filho (1977)
Sporolithon tenue Bahia, Amado-Filho, Maneveldt and Adey	Bahia et al. (2014b), Adey et al. (2015)*
Sporolithon amadoi	Richards et al. (2019)*
Sporolithon yoneshigueae	Bahia et al. (2015)*, Richards et al. (2017)*
CORALLINALES	
CORALLINACEAE	
Arthrocardia gardneri Manza#§	Oliveira Filho (1977)
Arthrocardia stephensonii Manza#§	Taylor (1960), Oliveira Filho (1977)
Corallina officinalis Linnaeus§	Taylor (1930), Oliveira Filho (1977), Moura (2000)
Jania adhaerens J.V.Lamouroux§#	Taylor (1930), Oliveira Filho (1977), Moura (2000)

Jania capillaceae Harvey§	Taylor (1960), Oliveira Filho (1977), Moura (2000), Villaça et al. (2010)
Jania cubensis Montagne ex Kützing §	Taylor (1930,1960), Oliveira Filho (1977), Moura (2000)
Jania prolifera A.B.Joly§	Joly (1965), Oliveira Filho (1977), Moura (2000)
Jania pumila J.V.Lamouroux§#	Taylor (1960), Oliveira Filho (1977), Moura (2000), Villaça et al. (2010)
Jania rubens (Linnaeus) J.V.Lamouroux §#	Taylor (1930), Joly (1957), Oliveira Filho (1977), Moura (2000), Villaça et al. (2010)
Jania subulata (Ellis and Solander) Sonder§	Taylor (1930), Oliveira Filho (1977), Moura (2000)
Neogoniolithon accretum (Foslie and Howe) Setch and Mason#	Figueiredo and Steneck (2002)
Neogoniolithon atlanticum Tâmega, Riosmena-Rodriguez, Mariath and Figueiredo	Tâmega et al. (2014)
Neogoniolithon brassica-florida (Harvey) Setchell and Mason	Villas-Bôas et al. (2015)
Neogoniolithon fosliei (Heydrich) Setchell and Mason	Taylor (1960), Oliveira Filho (1977)
Neogoniolithon mamillare (Harvey) Setchell and Mason#	Oliveira-Filho (1977)
Spongites fruticulosa Kützing	Tâmega et al. (2014)
Spongites yendoi (Foslie) Chamberlain	Henriques et al. (2012), Costa et al. (2014)
LITHOPHYLLACEAE	
Amphiroa anastomosans Weber Bosse§#	Oliveira (1977), Moura and Guimarães (2005), Torrano-Silva et al. (2018)* as *A. fragilissima*
Amphiroa beauvoisii J.V.Lamouroux§#	Oliveira (1977), Moura and Guimarães (2005), Torrano-Silva et al. (2018)*
Amphiroa brasiliana Decaisne§#	Taylor (1930), Joly (1965), Oliveira Filho (1977), Moura and Guimarães (2005)
Amphiroa fragilissima (Linnaeus) JV. Lamouroux§#	Taylor (1930), Oliveira Filho (1977), Moura and Guimarães (2005), Torrano-Silva et al. (2018)*
Amphiroa rigida J.V.Lamouroux§#	Oliveira Filho (1977), Moura and Guimarães (2005)
Amphiroa vanbosseae Me. Lemoine§#	Moura and Guimarães (2005), Torrano-Silva et al. (2018)*
Dawsoniolithon conicum (E.Y.Dawson) Caragnano, Foetisch, Maneveldt & Payri	Mariath et al. (2012), Jesoinek et al. (2016)*, Amado-Filho et al. (2018)

Harveylithon catarinense Costa, Horta and Nunes	Costa et al. (2019)*
Harveylithon maris-bahiensis Costa, Horta and Nunes	Costa et al. (2019)*
Harveylithon riosmenum Costa, Horta and Nunes	Costa et al. (2019)*
Harveylithon samoënse (Foslie) Rösler, Perfectti, Peña & Braga	Tâmega and Figueiredo (2005)
Hydrolithon boergesenii (Foslie) Foslie	Jesionek et al. (2016)*, Amado-Filho et al. (2018)
Hydrolithon breviclavium (Foslie) Foslie	Henriques et al. (2014b)
Hydrolithon farinosum (Lamouroux) Penrose and Chamberlain	Taylor (1960), Oliveira Filho (1977), Horta (2000)
Hydrolithon rupestre (Foslie) Penrose	Amado-Filho et al. (2012 a,b), Crespo et al. (2014), Villas-Bôas et al. (2015)
Lithophyllum atlanticum Vieira-Pinto, Oliveira and Horta	Vieira-Pinto et al. (2014)*, Torrano-Silva et al. (2018)*
Lithophyllum kaiseri (Heydrich) Heydrich	Figueiredo and Steneck (2002) as *L. congestum*, Jesionek et al. (2016)*
Lithophyllum corallinae (Crouan and Crouan) Heydrich	Henriques et al. (2014b), Torrano-Silva (2015)*
Lithophyllum depressum Villas-Boas, Figueiredo and Riosmena-Rodriguez	Villas-Bôas et al. (2009)
Lithophyllum johansenii Woelkerling and Campbell	Villas-Bôas et al. (2009)
Lithophyllum margaritae (Hariot) Heydrich	Horta (2000), Pascelli et al. (2013), Vieira-Pinto et al. (2014)*, Torrano-Silva et al. (2018)*
Lithophyllum stictaeforme (Areschoug) Hauck	Nunes et al. (2008), Villas-Bôas et al. (2009), Amado-Filho et al. (2012a), Pascelli et al. (2013), Costa et al. (2014), Henriques et al. (2014b)
Lithophyllum rugosum (Foslie) Me.Lemoine[#]	Pascelli et al. (2013)
Paulsilvella huveorum Woelkerling, Sartoni and Boddi[§]	Torrano-Silva et al. (2014)*
Pneophyllum fragile Kützing[#]	Taylor (1960), Oliveira Filho (1977), Bahia (2014)
Porolithon improcerum (Foslie and Howe) Lemoine	Bahia et al. (2014c), Mendes Crespo et al. (2014)
Porolithon onkodes (Heydrich) Foslie	Taylor (1960), Oliveira Filho (1977), Henriques et al. (2014b), Jesoinek et al. (2016)*
Porolithon antillarum (Foslie and M.Howe) Foslie and M.Howe	Tâmega et al. 2014 (as *P. pachydermum*)
Titanoderma prototypum (Foslie) Woelkerling, Chamberlain and Silva	Torrano-Silva (2015)*, Jesoinek et al. (2016)*
Titanoderma pustulatum (J.V. Lamouroux) Nägeli	Oliveira Filho (1977), Torrano-Silva et al. (2018)*

HAPALIDIALES	
HAPALIDIACEAE	
Lithothamnion brasiliense Foslie#	Taylor (1930), Oliveira Filho (1977), Costa et al. (2014)
Lithothamnion crispatum Hauck#	Costa et al. (2014), Jesionek et al. (2016)*
Lithothamnion glaciale Kjellman	Costa et al. (2014)
Lithothamnion muelleri Lenormand ex Rosanoff	Costa et al. (2014)
Lithothamnion occidentale (Foslie) Foslie#	Oliveira-Filho (1977)
Lithothamnion sejunctum Foslie#	Wynne (2017)
Lithothamnion steneckii Mariath and Figueiredo	Mariath et al. (2012)
Melobesia membranacea (Esper) Lamouroux	Taylor (1960), Oliveira Filho (1977), Borges et al. (2014)
Melobesia rosanoffii (Foslie) Lemoine	Borges et al. (2014)
Mesophyllum engelhartii (Foslie) Adey	Villas-Boas et al. (2014)
Melyvonnea erubescens (Foslie) Athanasiadis and Ballantine	Taylor (1930), Nunes et al. 2008 as *Mesophyllum erubescens*, Horta et al. (2011), Costa et al. (2014), Sissini et al. (2014)*, Jesionek et al. (2016)*
Mesophyllum macroblastum (Foslie) Adey	Bahia et al. (2014c)
Phymatolithon calcareum (Pallas) Adey and Mckibbin#	Taylor (1930), Oliveira Filho (1977) as *Lithothamnion polymorphum*
Phymatolithon masonianum Wilks and Woelkerling	Costa et al. (2014)
Tectolithon fluminense Bahia, Jesionek and Amado-Filho	Jesionek et al. (2020)*
Crustaphytum atlanticum Jesionek, Bahia and Amado-Filho	Jesionek et al. (2020)*

Table S2: Environmental variables considered as potential predictors of coralline red algae richness based on Carvalho et al. (2019). In bold, the eight selected variables by tha DistLM analysis. Data were obtained from surface layers for occurrences down to 10 meters deep, available in BioOracle (www.bio-oracle.org, Tyberghein et al. 2012; Assis et al. 2018).

Environmental predictor	Unit
Long-term max. Current Velocity	**m^{-1}**
Long-term min. Current Velocity	**m^{-1}**
Long-term max. Nitrate concentration	$mmol.m^{-3}$
Long-term min. Nitrate concentration	$mmol.m^{-3}$
Photosynthetically Active Radiation max.	$E.m^{-2}.day^{-1}$
Photosynthetically Active Radiation mean	$E.m^{-2}.day^{-1}$
Long-term max. Phosphate concentration	**$mmol.m^{-3}$**
Long-term min. Phosphate concentration	**$mmol.m^{-3}$**
Long-term min. Salinity	**Psu**
Long-term max. Ocean Temperature	**ºC**
Long-term min. Ocean Temperature	**ºC**
pH	-

Table S3: Jaccard beta diversity (β_{JAC}, in bold) decoupled in its respective turnover ($\beta_{turnover}$, in italic) and nestedness ($\beta_{nestedness}$, in normal caps) components among Southwestern Atlantic ecoregions, according Spalding et al. (2007).

	Amazonia	Fernando de Noronha.and.Rocas	Northeastern Brazil	Eastern Brazil	Trindade and Martin Vaz Islands
Fernando de Noronha and Rocas	**0.87** (*0.75*/0.12)				
Northeastern Brazil	**0.88** (*0.57*/0.31)	**0.87** (*0.80*/0.07)			
Eastern Brazil	**0.96** (*0.75*/0.21)	**0.85** (*0.50*/0.35)	**0.78** (*0.61*/0.17)		
Trindade and Martin Vaz Islands	**1.00** (*1.00*/0.00)	**0.83** (*0.80*/0.03)	**0.90** (*0.80*/0.10)	**0.93** (*0.71*/0.21)	
Southeastern Brazil	**1.00** (*1.00*/0.00)	**0.97** (*0.96*/0.01)	**0.86** (*0.85*/0.01)	**0.74** (*0.58*/0.16)	**0.97** (*0.94*/0.03)

Table S4: Values of significance of Monte Carlo to PERMANOVA based on Sorensen's similarity using 999 permutations showing the differences between the ecoregions with respect to CRA richness. * indicates significantly different ecoregions based on biological variables.

Groups	P(MC)
Eastern Brazil, Southeastern Brazil	0.001*
Eastern Brazil, Northeastern Brazil	0.001*
Eastern Brazil, Fernando de Noronha and Rocas Atoll	0.433
Eastern Brazil, Trindade and Martin Vaz Islands	0.033
Eastern Brazil, Amazonia	0.551
Southeastern Brazil, Northeastern Brazil	0.001*
Southeastern Brazil, Fernando de Noronha and Rocas Atoll	0.162
Southeastern Brazil, Trindade and Martin Vaz Islands	0.031
Southeastern Brazil, Amazonia	0.407
Northeastern Brazil, Fernando de Noronha and Rocas Atoll	0.123
Northeastern Brazil, Trindade and Martin Vaz Islands	0.031
Northeastern Brazil, Amazonia	0.781
F. de Noronha and Rocas Atoll, Trindade and Martin Vaz Is.	0.214
Fernando de Noronha and Rocas Atoll, Amazonia	0.437
Trindade and Martin Vaz Islands, Amazonia	0.264

Table S5: Percentage of variation explained by individual axes in the redundancy analysis (dbRDA) when integrating patterns of coralline algae richness distribution and its relationship with the environmental drivers. Results of the distance-based multivariate multiple regression (DistLM) of CRA ocurrence data overlaid with the partial correlations of the significant environmental variables identified by the best models using the AICc criterion.

Axis	% explained variation out of fitted model		% explained variation out of total variation	
	Individual	Cumulative	Individual	Cumulative
1	41.59	41.59	6.05	6.05
2	16.63	58.21	2.42	8.46
3	13.71	71.92	1.99	10.46
4	11.04	82.96	1.61	12.06
5	5.93	88.89	0.86	12.92
6	5.15	94.04	0.75	13.67
7	3.78	97.82	0.55	14.22
8	2.18	100	0.32	14.54

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SUPPLEMENTARY FIGURES

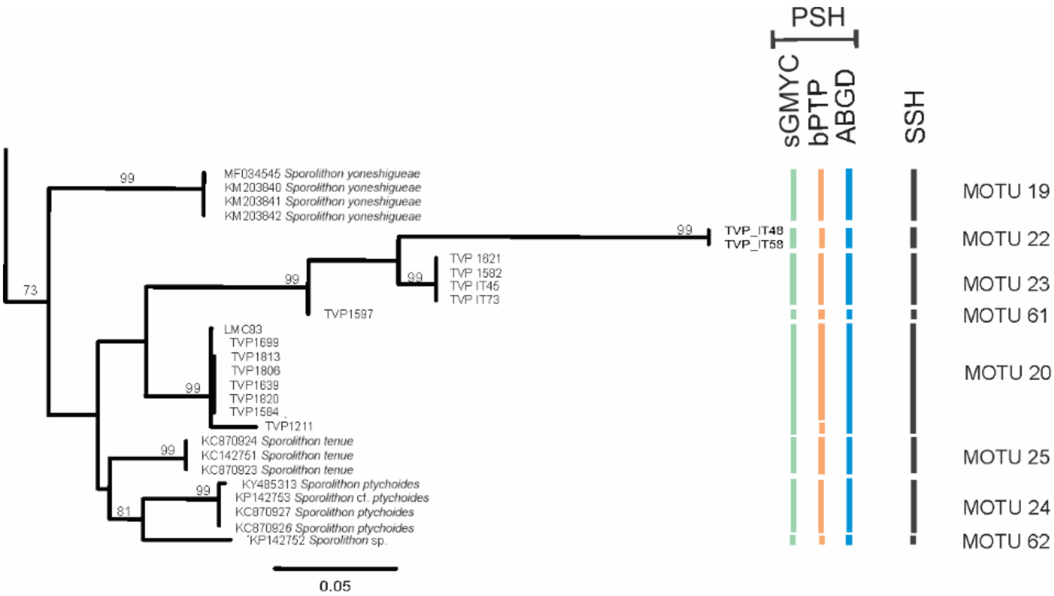


Fig. S1 Maximum likelihood *psb*A tree for Sporolithales in the Southwestern Atlantic Ocean. Numbers in the branches are Maximum likelihood (ML) bootstrap values. Bars represent the three species delimitation methods: in green the single threshold Generalized Mixed Yule Coalescent (sGMYC), in orange the Bayesian Poisson-Tree Processes (bPTP) and, in blue, Automatic Barcode Gap Discovery (ABGD). These three methods tested the Primary Species Hypothesis (PSH) and the consensus between two or more methods defined Secondary Species Hypothesis (SSH), represented by the gray bars.

Fig. S2 Maximum likelihood *psb*A tree for Corallinales in the Southwestern Atlantic Ocean. Numbers in the branches are Maximum likelihood (ML) bootstrap values. Bars represent the three species delimitation methods: in green the single threshold Generalized Mixed Yule Coalescent (sGMYC), in orange the Bayesian Poisson-Tree Processes (bPTP) and, in blue, Automatic Barcode Gap Discovery (ABGD). These three methods tested the Primary Species Hypothesis (PSH) and the consensus between two or more methods defined Secondary Species Hypothesis (SSH), represented by the gray bars.

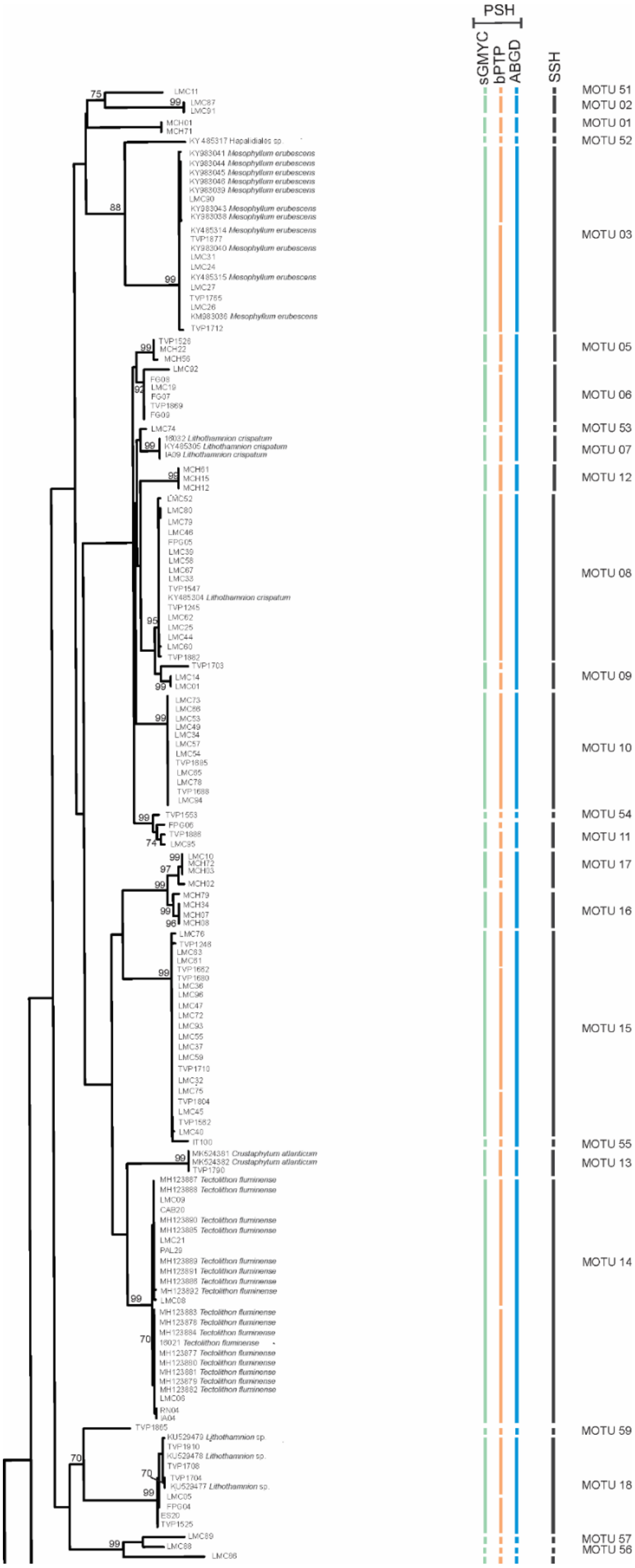
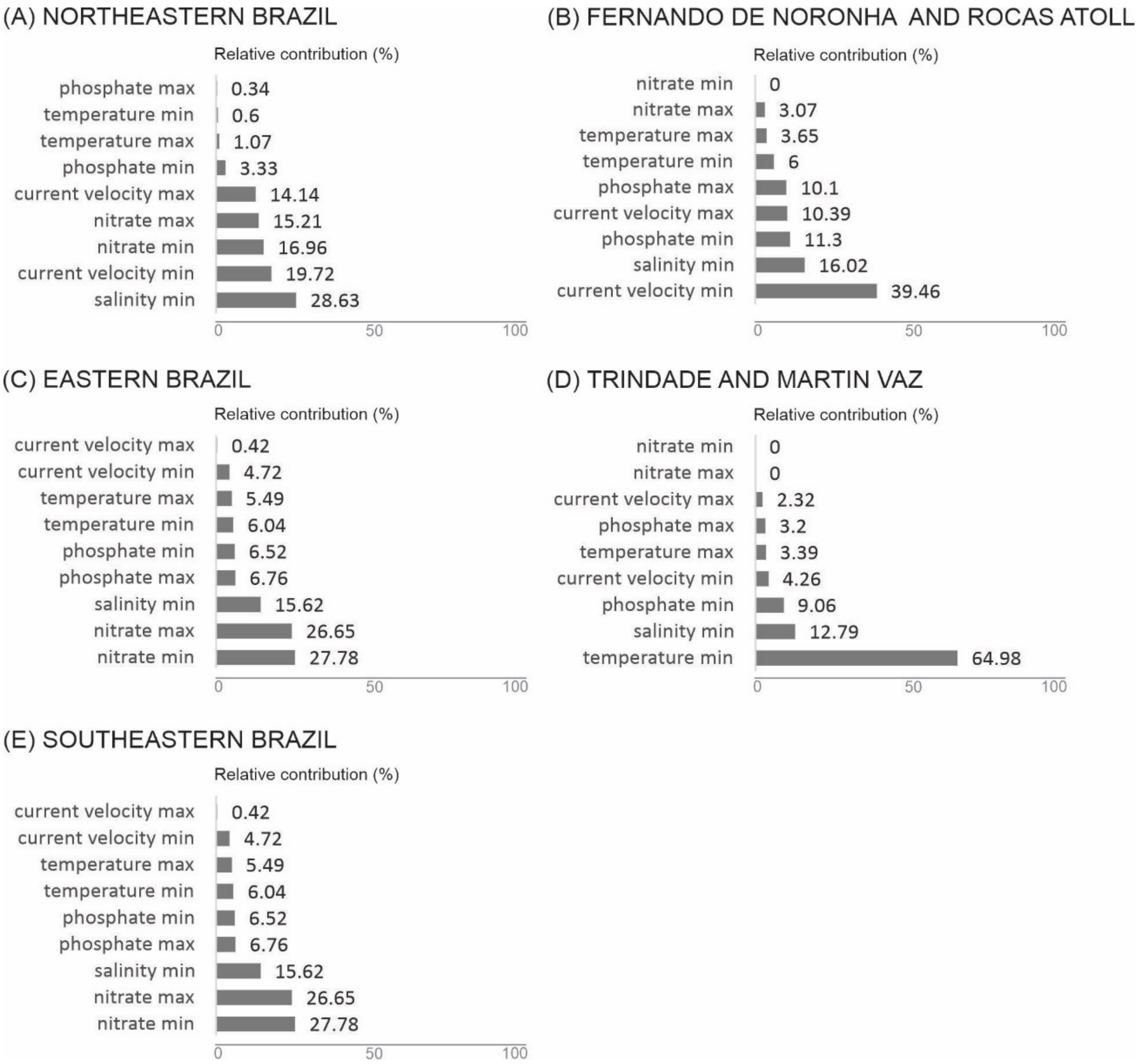


Fig. S3 Maximum likelihood *psb*A tree for Hapalidiales in the Southwestern Atlantic Ocean. Numbers in the branches are Maximum likelihood (ML) bootstrap values. Bars represent the three species delimitation methods: in green the single threshold Generalized Mixed Yule Coalescent (sGMYC), in orange the Bayesian Poisson-Tree Processes (bPTP) and, in blue, Automatic Barcode Gap Discovery (ABGD). These three methods tested the Primary Species Hypothesis (PSH) and the consensus between two or more methods defined Secondary Species Hypothesis (SSH), represented by the gray bars.



(A) NORTHEASTERN BRAZIL

(B) FERNANDO DE NORONHA AND ROCAS ATOLL

(C) EASTERN BRAZIL

(D) TRINDADE AND MARTIN VAZ

(E) SOUTHEASTERN BRAZIL

Fig. S4 Relative importance of environmental variables in the similarity within each ecoregion evidenced by SIMPER analysis. **(A)** Northeastern Brazil, **(B)** Fernando de Noronha and Rocas atoll, **(C)** Eastern Brazil, **(D)** Trindade and Martin Vaz Islands, **(E)** Southeastern Brazil. Unity of environmental variables: salinity in PPS, current velocity in m^{-1}, phosphate and nitrate concentration in mmol.m^{-3} and temperature in ºC. Data for the Amazonia ecoregion is not available as there were less than two samples in the group.

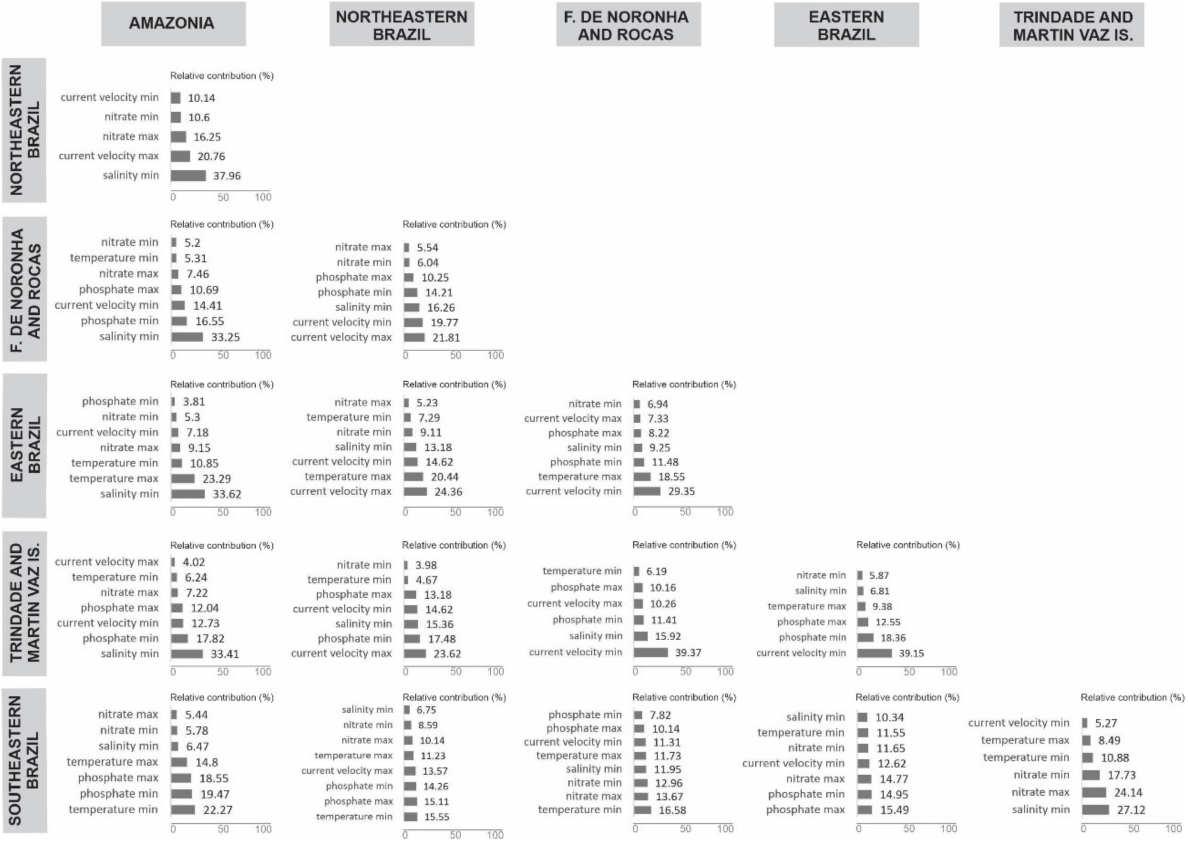


Fig. S5 Relative importance of environmental variables in the dissimilarity between ecoregions evidenced by SIMPER analysis.

SUPPLEMENTARY MATERIAL

SM 1. New collections

Encrusting specimens were collected with the help of a sledgehammer and a tip. In depths greater than 3 meters, samples were collected by SCUBA diving and, at depths greater than 30 meters, through dredging. Immediately after sampling, specimens were cleaned to remove epiphytes and associated fauna, and stored appropriately for morphological and molecular studies. For molecular analyses, material was dried in the shade and stored in silica gel. Specimen data including field codes and locations of sampling are shown in Table S2. Specimens were deposited in the Brazilian herbaria: FLOR of Federal University of Santa Catarina, R of the Rio de Janeiro National Museum, SPF of the University of São Paulo and ALCB of Federal University of Bahia (Index Herbariorum, http://sciweb.nybg.org/science2/IndexHerbariorum.asp).

SM 2. DNA sequencing

DNA extraction was performed using the NucleoSpin Plant II kit (Macherey-Nagel, Düren, Germany), DNeasy Plant Mini kit (Qiagen, Germany) according to the manufacturer's protocol, or the Chelex protocol (Goff and Moon 1993). The *psb*A was amplified by PCR and sequenced as described in Sissini et al. (2014). DNA sequencing was done at São Paulo University, Myleus facility (Brazil) or Macrogen Inc. (South Korea) using BigDye V3.1 kit and injected into an ABI 3730 equipment (Life Technologies/Thermo Fisher Scientific). Sequences were aligned and edited in BioEdit version 5.0.6 (Hall 1999). Chromatograms were visually inspected for validation of ambiguous nucleotides before generating a consensus sequence.

SM 3. Species delimitation and phylogenetic analyses

ML analyses as implemented in RAxML on the CIPRES Science Gateway v. 3.3 (Miller et al. 2010). RAxML analyses used 1,000 restarts and 1,000 bootstrap (BS) replications.

Three analyses for species delimitation were used to assess the number of species included in our *psb*A dataset: the Automatic Barcode Gap Discovery (ABGD, Puillandre et al. 2012), the Bayesian implementation of the Poisson Tree Processes model (bPTP, Zhang et al. 2013) and the General Mixed Yule Coalescent (sGMYC, Fujisawa and Barraclough 2013).

The ABGD method was performed in the web interface (http://wwwabi.snv.jussieu.fr/public/abgd/). The results of analyses performed under Jukes-Cantor 1969 (JC69) to calculate pairwise distances under the following optimum parameter values: Pmin=0.001, Pmax=0.1, recursive steps=10, X (relative gap width=1.0) and Nb bins=20. The bPTP method was performed in the online server (https://species.h-its.org/ptp/). A total of 500.000 MCMC generations with a thinning value of 100, 0.5 burn-in, and seed=123 were run.

The GMYC model used an ultrametric tree, generated in BEAST v2.6.0 (Bouckaert et al. 2014) estimated with a lognormal relaxed clock and using a constant population coalescent as prior. Two MCMC analyses were run for 100 million generations, sampling every 1000th generation. The quality of the run was assessed in Tracer v1.6 (Rambaut et al. 2014) to ensure that ESS values were > 200 with the default burn-in (100000 trees). The information from a sample of trees was summarized using Tree Annotator v 2.6.0 with 10% burn-in discarded, 0.5 of posterior probability (PP) limit. GMYC analyses were made using the packages “ape”, “paran” and “splits” in R version 3.1.2 (R Core Development Team 2014, available at http://www.R-project.org).

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CAPÍTULO 2

SPOROLITHALES FROM TROPICAL ATLANTIC - PHYLOGENETIC HISTORY AND EVOLUTION

(manuscrito a ser submetido ao periódico *Phycologia*)

formatação de acordo com as regras da revista

3. CAPÍTULO 2: SPOROLITHALES FROM TROPICAL ATLANTIC - PHYLOGENETIC HISTORY AND EVOLUTION

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ABSTRACT

Speciation is still one of the significant challenges for understanding evolution in the marine environment. Recent phylogeographic studies have highlighted important and less popular evolutionary mechanisms and different, but not self-excluding, hypotheses have been tested to explain the high biodiversity found in tropical marine environments, such as “the center of speciation”, “the center of accumulation” and “the center of overlap”. Studies testing these hypotheses with macroalgae are scarce and even rarer those that explore the origin of the phycoflora in the Atlantic Ocean. Here we assemble the first comprehensive worldwide distribution of Sporolithales, focusing on the history of the SWA’s Sporolithales with other marine realms and provinces. Through species delimitation methods based on DNA sequences, we found 23 molecular operational taxonomic units of Sporolithales, distributed in nine marine realms, with the Tropical Atlantic being the most specious. The geographic distribution of Sporolithales is restricted to ocean basins. Most species (*i.e.*, 83% of 23 species) occur in an unique biogeographic province, suggesting a high level of regional endemism. Groups currently distributed in tropical and sub-polar environments, show ecophysiological affinities that enabled the colonization and survival in mesophotic environments. The results obtained in this study show that *Sporolithon* species occurring in the SWA originated at different places and times, and the Caribbean may have acted as a center of dispersion. In our calibration, diversification in Sporolithales has been constant over time and increased from the Neogene. Adaptations to current mesophotic conditions might account for the survival of Sporolithales in times less favorable to life, such as after mass extinctions.

Keywords: marine biogeography, species delimitation methodos, speciation, macroevolution, *Sporolithon*.

3.1 INTRODUCTION

Understanding speciation remains a significant challenge for describing evolution in the marine environment (Mayr 1954; Palumbi 1992; Miglietta et al. 2011; Faria et al. 2021). Phylogeographic studies have revealed processes of diversification in the oceans, overturning ingrained assumptions (Mc Coy & Heck 1983; Choat 2006; Bowen et al. 2013). Among them, we can mention that: (i) physical isolation (allopatric speciation) is not the only path to speciation, as many species diverge due to physiological/ecological filters and, potential cases of sympatric speciation have already been verified in limpets (Bird 2011) and reef fishes (Crow et al. 2010); (ii) peripheral environments, such as oceanic islands, and boundary areas of species distribution, such as transition zones, are not evolutionary cemeteries as previously stated, these regions can accumulate, or even export biodiversity (Bellemain & Ricklefs 2008; Bowen et al. 2013; Pinheiro et al. 2017; Harvey et al. 2020) and, (iii) biodiversity hotspots, such as the Caribbean Sea and the Indo-Malay Archipelago, produce and export species, but can also receive and harbor biodiversity produced in peripheral habitats (Palumbi 1996; Meyer et al. 2005; Rocha et al. 2008a).

Among the processes that can explain high speciation rates in tropical marine environments, three hypotheses, not self-excluding, stand out: “the center of speciation” (Darwin 1859; Briggs 2005), “the center of accumulation” (Connolly et al. 2003) and “the center of overlap” (Hobbes 2009). The center of speciation hypothesis postulate that, in the center, species originate and then disperse to the periphery, with the high diversity in the center being the result of speciation in situ (Darwin 1859; Briggs 2005). The center of accumulation theory, on the other hand, suggests that the diversity centers accumulate species that originated elsewhere (Connolly et al. 2003). Further, the center of overlap suggests that isolated fauna present their distribution limit in a common region with the co-occurrence of sister species in the center of overlap (Hobbes 2009; Bowen et al. 2013). In this way, when phylogeographic studies detect more recent lineages or species in biodiversity hotspots, the center of speciation hypothesis is endorsed. In the same way, the hypotheses of center of accumulation and/or overlap is corroborated when more recent lineages or species are found in peripheral areas (Rocha et al. 2008a; Bowen et al. 2013).

In the marine realm, phylogeographic studies show that different evolutionary mechanisms occur in different species of reef fishes (Muss et al. 2001; Rocha 2003; Bowen et al. 2006; Rocha et al. 2008a; Pinheiro et al. 2017; Liedke et al. 2020). Rocha et al. (2008a) verified for *Chromis multilineata* that the oldest lineages in the Atlantic were identified for the Caribbean, corroborating the hypothesis of center of origin. However, haplotypes from Brazilian lineages have also been found in populations from the Caribbean, showing that this region is also a center of accumulation. Among the brown algae, historical biogeographic analyzes corroborated the center of speciation hypothesis in *Dictyota*, whereas for *Lobophora* it was found that this genus both originated in the tropics and remained there (accumulation hypothesis, Vieira et al. 2021). Studies with macroalgae testing the hypotheses of the origin of biodiversity are scarce (Verbruggen et al. 2009; Leliaert et al. 2018; Vieira et al. 2021) and even rarer those that explore the origin of the phycoflora in the Atlantic ocean. Calcareous algae have all the requirements for a model organism for biogeographic and evolutionary: **(i)** a wide distribution (Foster 2001); **(ii)** high species diversity, comprise the third most diverse group among the rhodophytes of the current seas, with approximately 750 recognized morpho-species (Guiry & Guiry 2021); **(iii)** a good preservation in the fossil record, which enables phylogenetic calibration (Aguirre et al. 2010) and, **(iv)** they are ancient organisms, whose origin has already been estimated for the beginning of the Cambrian (Yang et al. 2016), having been exposed to various selective pressures in a wide range of time (Peña et al. 2020).

Coralline red algae occupy a wide range of marine environments, occuring from the poles to the tropics in tidal pools, biogenic reefs, rocky reefs, and from the supralittoral to the mesophotic habitats in the ocean (Littler et al. 1985; Littler et al. 1983; Nelson 2009). Differently from other tropical seas, the Southwestern Atlantic (SWA) reefs revealed CRA as dominant, diverse and key organisms (Leão et al. 2003; Meirelles et al. 2015; Moura et al. 2016; Aued et al. 2018; Bastos et al. 2018; Sissini et al. submitted). This suggests that the SWA might have unique characteristics that are likely to be important in terms of ecosystem functions and services, and understanding how species vary is essential to understanding how these organisms, and the environments built by them, will respond to future climate change scenarios (Rindi et al. 2019).

The patterns of geographic distibution in CRA are greatly influenced by environmental conditions, as temperature (Adey & Steneck 2001; Peña et al. 2015; Carvalho et al. 2020; Sissini et al. submitted), current velocity (Basso et al. 2009; Carvalho et al. 2020; Sissini et al. submitted), irradiance (Wilson et al. 2004) and sedimentation rates (Riul et al. 2008). These macroecological evaluations provide a perspective on the conditions currently limiting the species distribution, *e.g.*, physiological requirements and/or biological interactions (Wiens &

Donoghue 2004). However, to understand aspects related with distribution patterns, we also need to consider historical evolutionary events responsible for the regional species pool, as dispersal capacity, extinction and vicariant processes (Cowie & Holland 2006; Verbruggen et al. 2009). Dispersal limitations imposed by biogeographical barriers in the Tropical Atlantic have been demonstrated as permeable filters that can restrict movement, only allowing occasional crossings that can lead to the establishment of new populations and species [*e.g.*, reef fishes (Rocha 2003; Floeter et al. 2008; Anderson et al. 2017); corals (Souza et al. 2017); and macroalgae (Nauer et al. 2015)]. However, there is no information about how these barriers affect CRA and how they shape patterns of diversity. Moreover, knowledge about the dispersal strategies of CRA is pratically non existent. What is known, however, is that CRA, as well as other red algae, do not present structures that increase their dispersal, such as flagella and the dispersion of this group is largely dependent on water movements (Pueschel 1989; Kinlan & Gaines 2003, Tâmega et al. 2016). However, the ability to encrust movil substrates, both natural (other pelagic macroalgae, tree trunks, turtle shells) and artificial surfaces (line, boat hull) enhances their dispersal potential, over long distances (Kinlan & Gaines 2003; Bryan et al. 2012; Fraser et al. 2018).

Among the groups of CRA, the order Sporolithales hosts the oldest representatives. Currently, 40 living species are taxonomically recognized occurring worldwide (Guiry & Guiry 2021), most only morpho-anatomically characterized. In the Tropical Atlantic, Sporolithales is represented by the genus *Sporolithon*, with 14 species, of which only seven species were described based on molecular data: *S. franciscanum* (Leão et al. 2020), *S. tenue* (Bahia et al. 2013), *S. yoneshigueae* (Bahia et al. 2015), *S. amadoi* (Richards et al. 2019), *S. mesophoticum* (Richards et al. 2019), *S. sinusmexicanum* (Richards et al. 2018), *S. episporum* (Richards et al. 2017) As CRA have few diagnostic characters, it was believed that the phenotypic variability of similar morphologies was due to adaptations to different environmental conditions (Steneck & Adey 1976; Woelkerling et al. 1993). However, with the widespread use of molecular tools, studies have shown restricted species distributions and recurrent cryptic diversity cases (*e.g.*, Sissini et al. 2014; Gabrielson et al. 2018; Torrano-Silva et al. 2018; Twist et al. 2019), and DNA-based identifications are strongly recommended (Twist et al. 2020).

Investigating the evolutionary history of Sporolithales can illuminate how past climates, geochemical changes and ocean circulation shaped the persistence and evolution of this group, and thus inform predictions of the future of coralline ecosystems (Rindi et al. 2019).

Here we assemble the first comprehensive analysis of the global distribution of Sporolithales, focusing on describing the history of the Tropical Atlantic's species with other marine realms and provinces. Moreover, we aim to investigate patterns of species origination by using a time-calibrated phylogenetic framework for Sporolithales.

3. 2 MATERIAL AND METHODS

3.2.1 Database

We employed the concept of Molecular Operational Taxonomic Unit (MOTU, Floyd et al. 2002), given the difficulty in identifying CRA species based on morphology. Therefore, only records with DNA sequences were considered. In this study, we chose the *psb*A marker, since it is the most widely used for CRA groups and has shown enough interspecific variation for species delimitation (*e.g.*, Sissini et al. 2014; Vieira-Pinto et al. 2014; Richards et al. 2019; Twist et al. 2019). We built an initial alignment with all the Sporolithales sequences available from GenBank until the date of analysis (22 October 2020) and then we discard those without location information.

3.2.2 DNA-based species delimitation and phylogenetic analyses

Maximum Likelihood analyses as implemented in RAxML on the CIPRES Science Gateway v. 3.3 (Miller et al. 2010). RAxML analyses used 1,000 restarts and 1,000 bootstrap (BS) replications. Results were visualized in FigTree v. 1.4.2 (Rambaut 2014).

Three analyses for species delimitation were used to assess the number of species included in our *psb*A dataset: the Automatic Barcode Gap Discovery (ABGD, Puillandre et al. 2012), the Bayesian implementation of the Poisson Tree Processes model (bPTP, Zhang et al. 2013) and the General Mixed Yule Coalescent (sGMYC, Fujisawa & Barraclough 2013).

The ABGD method was performed in the web interface (http://wwwabi.snv.jussieu.fr/public/abgd/). The results of analyses performed under Jukes-Cantor 1969 (JC69) to calculate pairwise distances under the following optimum parameter values: Pmin=0.001, Pmax=0.1, recursive steps=10, X (relative gap width=1.0) and Nb bins=20. The bPTP method was performed in the online server (https://species.h-its.org/ptp/). A total of 500.000 MCMC generations with a thinning value of 100, 0.5 burn-in, and seed=123 were run.

The GMYC model used an ultrametric tree, generated in BEAST v2.6.0 (Bouckaert et al. 2014) estimated with a lognormal relaxed clock and using a constant population coalescent as prior. Two MCMC analyses were run for 100 million generations, sampling every 1000th generation. The quality of the run was assessed in Tracer v1.7 (Rambaut et al. 2018) to ensure that ESS values were > 200 with the default burn-in (100000 trees). The information from a sample of trees was summarized using Tree Annotator v 2.6.0 with 20% burn-in discarded, 0.5 of posterior probability (PP) limit. GMYC analyses were made using the packages "ape", "paran" and "splits" in R version 3.1.2 (R Core Development Team 2014, available at http://www.R-project.org).

3.2.3 Geographical distributions

The occurrence data were obtained from an exhaustive literature review. Only occurrences with DNA sequences were considered to avoid taxonomic biases. We used the concept of Molecular Operational Taxonomic Unit (MOTU, Floyd et al. 2002) to define the smallest taxonomic entity. A total of 93 occurrences were compiled and were divided by realms and biogeographic provinces, according to Spalding et al. (2007).

3.2.4 Time calibrated phylogeny

The species phylogeny was based on an alignment for each species identified in the SDM analyzes for the *psb*A marker. Substitution models were estimated prior to the analysis with jModelTest2 2.1.6 on XSEDE (Darriba et al. 2011), executed on the CIPRES Science Gateway v3.3 (Miller et al. 2010). GTR+I+G was the preferred model for *psb*A via the Akaike Information Criterion (AIC). Maximum likelihood (ML) and Neighbor Joining (NJ) analysis were performed in MEGA with 1000 bootstrap support (BS) replicates. Bayesian inference (BI) analysis was conducted using MrBayes 3.2.6 (Huelsenbeck & Ronquist 2001) under the same model (GTR+ I+G) with four independent Markov Chain Monte Carlo (MCMC) runs off one million generations each, and sampling trees every thousand generations. The first 25% generations were discarded as burn-in.

A time-calibrated Bayesian phylogeny of Sporolithales was constructed with BEAST 1.8.2 (Drummond et al. 2012). The age of the nodes was estimated based on the Corallinales time-calibrated phylogeny of Peña et al. (2020) and in a database of fossil CRA based on a literature survey compiled by Juan C. Braga and Julio Aguirre. Four calibration nodes were strategically placed in disparate regions of the tree: A: Hapalidiales (116.66 Ma ± 0.66); B: Sporolithales (137.63 Ma ± 1.23); C: *S. episporum* (1.5 Ma ± 1.0); D: *S. erythraeum* (3.9 Ma ± 1.5). The absolute age attributed to each record was calculated as the midpoint of the absolute age range of the stratigraphic interval from which the taxon was reported, according to the International Chronostratigraphic Chart (Cohen et al. 2013).

The chronogram was built using a Birth-Death tree prior (Gernhard 2008), an uncorrelated lognormal (UCLN) relaxed clock model of rate variation among branches (Drummond et al. 2006) with the mean of the branch rates (ucld.mean) estimated with a lognormal distribution prior (shape 0.001, scale 1,000). All other priors were left as default. Four independent MCMC analyses of 20 million generations were performed, sampling every 2,000 generations, to obtain posterior distributions of parameters excluding a burn-in of 10%. Convergence of each analysis was determined in TRACER 1.6 (Rambaut et al. 2014), examining the effective sample size for all parameters. MCMC analyses were combined in LogCombiner 1.8.2, and maximum clade credibility trees were generated with TreeAnnotator. FigTree 1.4.2 (Rambaut 2014) was used to visualize the chronogram.

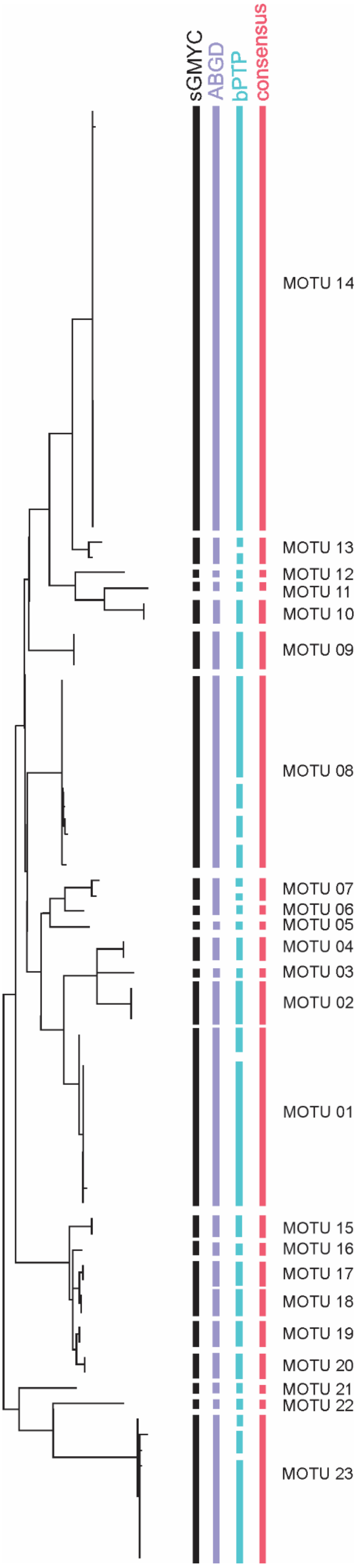
3.2.5 Ancestral state estimation

We use a representative of each species delimited by the methods described in section *3.2.2* section, by realm, for the construction of an ultrametric tree in the BEAST program. For the distribution character, nine states were delimited. The MOTUS occurrence matrix by realm was assembled for the reconstruction of the ancestral character using Maximum Parsimony (MP) in Mesquite version 3.61 (Maddison & Maddison 2019).

3.3. RESULTS

Diversity and distribution

Consensus of the three species delimitation methods revealed 23 species of Sporolithales (Figure 1).


sGMYC
ABGD
bPTP
consensus
MOTU 14
MOTU 13
MOTU 12
MOTU 11
MOTU 10
MOTU 09
MOTU 08
MOTU 07
MOTU 06
MOTU 05
MOTU 04
MOTU 03
MOTU 02
MOTU 01
MOTU 15
MOTU 16
MOTU 17
MOTU 18
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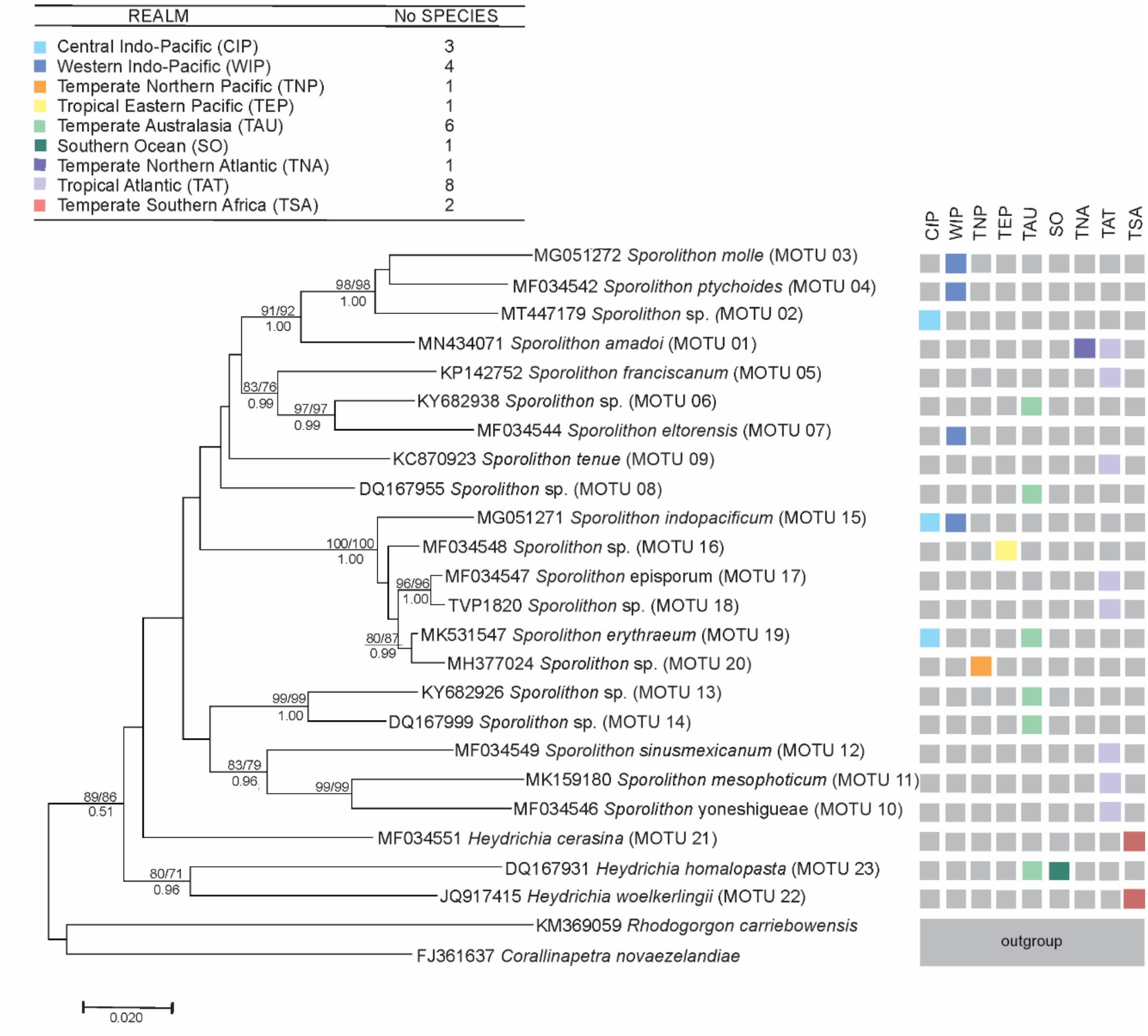
MOTU 20
MOTU 21
MOTU 22
MOTU 23

Figure 1. Maximum likelihood *psb*A tree for Sporolithales. Bars represent the three species delimitation methods: in black the single threshold Generalized Mixed Yule Coalescent (sGMYC), in purple Automatic Barcode Gap Discovery (ABGD) and, in green, the Bayesian Poisson-Tree Processes (bPTP). These three methods tested the Primary Species Hypothesis (PSH) and the consensus between two or more methods defined Secondary Species Hypothesis (SSH), represented by the red bars.

Extant Sporolithales species are distributed in nine realms: Central Indo-Pacific, Tropical Eastern Pacific, Western Indo-Pacific, Temperate Northern Pacific, Southern Ocean, Temperate Australasia, Temperate Northern Atlantic, Temperate Southern Africa, Tropical Atlantic. The richest realm is the Tropical Atlantic (eight species), followed by Temperate Australasia (six species) and Western Indo-Pacific (Figure 2).

Most species (78%) are distributed in a single realm and only five species (MOTU 1, 12, 15, 19, 23) are distributed in two realms. However, these realms are always located within the same oceanic basin.



REALM	No SPECIES
Central Indo-Pacific (CIP)	3
Western Indo-Pacific (WIP)	4
Temperate Northern Pacific (TNP)	1
Tropical Eastern Pacific (TEP)	1
Temperate Australasia (TAU)	6
Southern Ocean (SO)	1
Temperate Northern Atlantic (TNA)	1
Tropical Atlantic (TAT)	8
Temperate Southern Africa (TSA)	2

Figure 2. Neighbor Joining (NJ) phylogram based on *psbA* dataset. Numbers above branches are Neighbor-Joining (NJ)/ Maximum Likelihood (ML) bootstrap values over 75, number below branches are *Posteriori* Probability (PP) for Bayesian analysis. Scale bar represents the number of substitutions. Boxes represent the known geographical distribution of extant species.

In the province-level analyses (17 provinces), most species (16) were restricted to a single province, one species occurred in four provinces, and two species spanned two provinces (Table S1) .

Ancestral state estimation

None of the *Sporolithon* lineages from Tropical Atlantic have originated in other realms or have colonized the Atlantic realm. Our data show that the ancestral distribution, in all cases, was in the Tropical Atlantic (Figure 3).

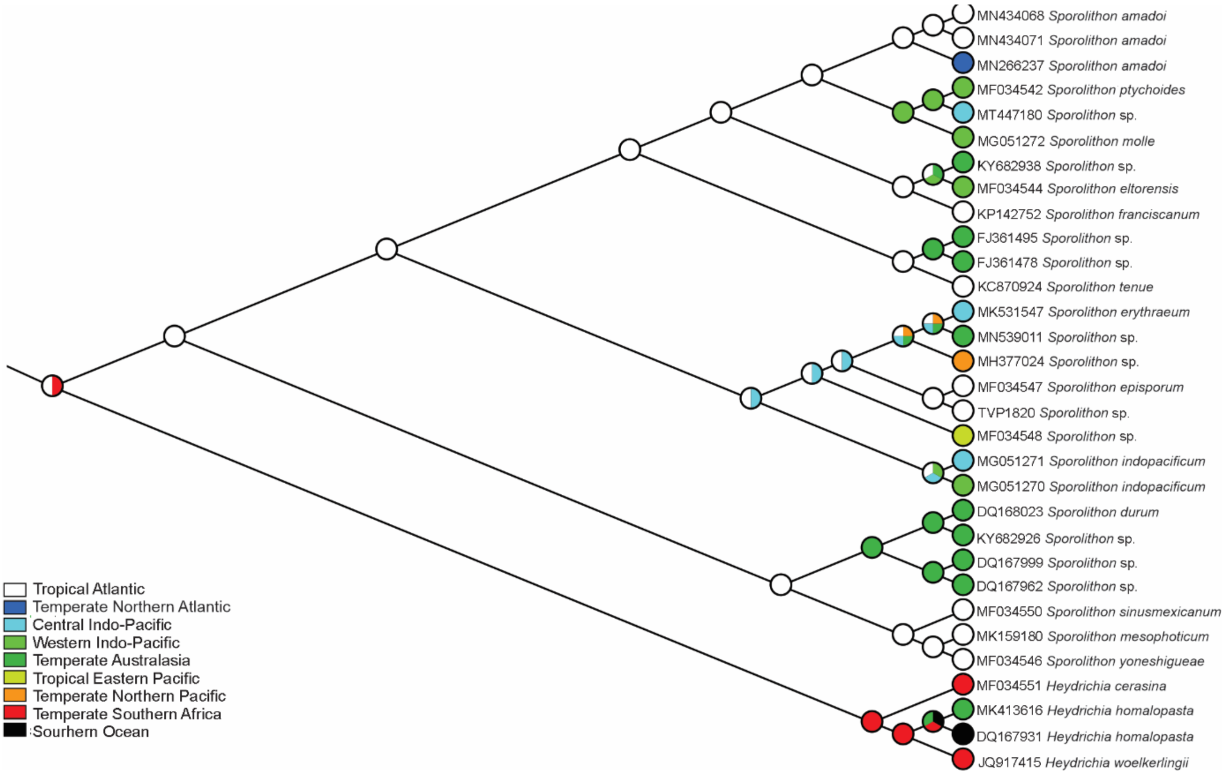


Figure 3. Ancestral state estimation under Maximum Parsimony (MP) over the Bayesian tree for the *psb*A molecular marker. The areas in the pie diagrams represent the relative support for each state reconstructed.

Time calibrated phylogeny

The origin of Sporolithales was estimated to have happened around the early Cretaceous [137.55 Ma (135.13–139.92 Ma, 95% highest posterior density, HPD); Figure 4]. The Brazilian coast has been colonized at least three times, in the Cretaceous (*S. tenue*), Eocene (*S. amadoi*, *S. franciscanum*, *S. yoneshigueae*) and Pleistocene (TVP1820).

Diversification of extant *Sporolithon* lineages occurred globally since the Albian (c. 114 Ma, 90.7–136.0 Ma, 95% HPD) until the Neogene (c. 2 Ma, 0.6–4.1 Ma, 95% HPD). In *Heydrichia*, occurred twice, in the late Cretaceous. The first in the Cenomanian (104.4 Ma, 72.5–131.5, 95% HPD) and the second in the Maastrichtian (68.6 Ma, 38.2–98.9, 95% HPD).

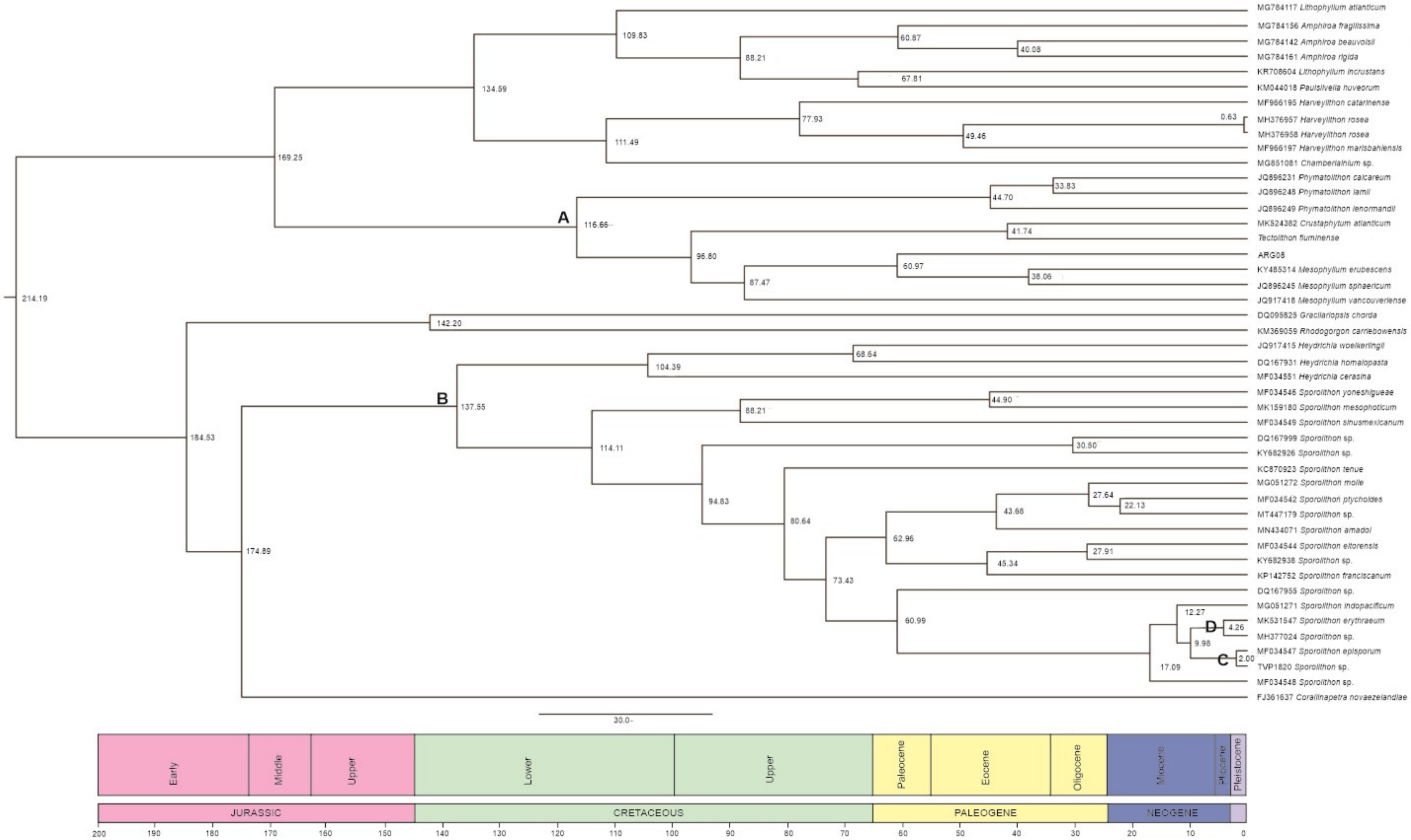


Figure 4. Time-calibrated phylogenetic tree of Sporolithales resulting from a BEAST analysis based on *psb*A. Four calibration points are indicated by the bold letters, A: Hapalidiales (116.66 ± 0.66); B: Sporolithales (137.63 ± 1.23); C: *S. episporum* (1.5 ± 1.0); D: *S. erythraeum* (3.9 ± 1.5).

3.4 DISCUSSION

Species diversity and biodiversity patterns

Our study revealed that, among the 23 MOTU of Sporolithales, which include widespread groups present from tropical to sub-polar regions, there are ecophysiological affinities or adaptative traits that allow them to colonize from shallow to mesophotic conditions. These CRA represent survivors which thrived in these refuges (Bongaerts & Smith 2019), surviving to the last mass extinction event, when stressors related to ocean warming and acidification reached values above the currently predicted to the end of this century (Quattrini et al. 2020). Time calibrated phylogeny indicated that the species occurring in the Tropical Atlantic appeared from the Late Cretaceous onwards and can have the dispersal centre in the Caribbean, as observed in *S. amadoi*, *S. yoshenigueae* and *Sporolithon* sp. (TVP1820).

Our calibration reinforces that diversification in Sporolithales has been constant over time and increased in the last periods from the Neogene (Fig. 4). Adaptations to mesophotic conditions might explain the survival of Sporolithales during the Cretaceous-Paleogene (K/Pg) transition (Aguirre et al. 2007). Aguirre et al. (2000) showed that the extinction rate among deep-water species was lower among Corallinales than Dasycladales, a group of calcifying green algae abundant in shallow waters during K/Pg. These authors suggested that Sporolithales were more successful after periods of a major disturbance, facilitating distributional expansion and the occupation of shallow environments. High diversification rates after the Cretaceous-Tertiary boundary were also observed for a group of brown algae that possible survived the conditions of darkness, global cooling and acid rain caused by the meteor impact and, thus, favoured opportunistic clades, such as *Lobophora* and *Dictyota* (Dictyotales) that occupied emptied niches (Vieira et al. 2021)

Relationships among species are congruent with previous studies (Bahia et al. 2014; Richards et al. 2017; Richards et al. 2019) and our estimate of the Sporolithales origin is similar to previous estimations (Aguirre et al. 2010; Yang et al. 2016; Peña et al. 2020). Time estimates should be considered carefully due to the incompleteness of the fossil record and the difficulties in identification of fossil species because of the lack of some characters useful for species delimitation. Sporolithales are present and abundant in the fossil record since the Cretaceous (Aguirre et al. 2000; 2010; Braga & Bassi 2007). *Sporolithon rude* from the early Hauterivian (~132 Ma, Arias et al. 1995) and *Sporolithon phylloideum* from the late Hauterivian (~129 Ma, Moussavian et al. 1993; Tomás et al. 2007) are the oldest feasibly identified species of the order.

Compared to other CRA orders, Sporolithales is the second less diverse, just behind the newly described Corallinapetrales (Jeong et al. 2021). This low species richness may be associated with a global temperature reduction recorded in the oceans by different paleotemperature estimates since 90 Ma (Aguirre et al. 2000; Braga & Bassi 2007). Braga & Bassi (2007) identified based on the number of species in the fossil record for the Mediterranean region an increase in the number of species during the Langhian. This increase is probably correlated with the mid-Miocene climatic optimum, that was followed by a drop in the species richness as consequence of the latter continuous cooling event up to the present day (Braga & Bassi 2007).

The geographic distribution of the Sporolithales species is restricted to ocean basins. Most species (*i.e.*, 83% of 23 species) occur in a unique biogeographic province, suggesting a high level of regional endemism. Although sampling efforts are greater at provinces in the Temperate Australia, as evidenced by our results, extant species of Sporolithales appear to have tropical affinities (Fig. 2, Table S2).

Sporolithales from Southwestern Atlantic

The result of our calibrated phylogeny revealed that the species currently occurring in the SWA have originated at different times, most likely with the Caribbean as the dispersing center. Global events around 80 Ma, 45 Ma and 17 Ma were responsible for evolutionary forces that reflected in the group's speciation process.

Sporolithon tenue originated in the Late Cretaceous (~90 Ma) and its current occurrence is restricted to Tropical SWA. The oldest CRA fossil found in Brazil, *Lithothamnion angolense*, is from the Sergipe Basin (Granier et al. 1991), found in the Albian strata. Woekerling et al. (2014), based on the presence of the Rio Grande Rise-Walvis System (RWS), suggested that a CRA fossil (taxon identification remains inaccurate, Peña et al. 2020) from Lower Cretaceous in Brazil would have its origin from the Central Atlantic rather than the South Atlantic. Although, the connection between the South and Central Atlantic was already possible at this time through shallow water (Dingle 1999; Pérez-Díaz & Eagles 2017), the Rio Grande-Walvis Ridge System imposed a physical barrier hindering deep ocean circulation (Graça et al. 2019). Until about 80 million years ago, the Rio Grande Rise was close to the Walvis Ridge, forming a 3000 km emerged mountain chain (Graça et al. 2019). Studies with ostracod distribution (Dingle 1999), paleobathymetry (Müller et al. 2008) and Nd-isotope signal (Voigt et al. 2013) reinforce, by different techniques, the role of the RWS in separating the North and South Atlantic basin until the late Maastrichtian. The emergence of a single water mass connecting the region above the Walvis Ridge originated in deep waters of the Southern Ocean, which occurred just after the Paleocene-Eocene (Thomas & Via 2007).

Sporolithon amadoi and *S. franciscanum* had estimated origin in the Eocene (Lutetian). The origin of these clades around 66 Ma corresponds to the end-Cretaceous (Cretaceous/Paleogene – K/Pg) mass extinction period, in which 70% of the calcareous algae species were extinguished due to the reduction in incident light on the seafloor (Aguirre et al. 2000; Braga & Bassi 2007). Nevertheless, the high species richness in carbonate sediments in India reveals the Sporolithales as capable of occupying and diversifying in disturbed environments, even after mass extinction events, such as the K/Pg (Ghosh & Sarkar 2013). *Sporolithon amadoi* and *S. franciscanum* have been described for mesophotic environments (Richards et al. 2019; Leão et al. 2020, Table S1). The high abundance of CRA in mesophotic environments from different regions of the world (*e.g.*, Brazil, Meirelles et al. 2015; Guabiroba et al. submitted; Bermudas, Goodbody-Gringley et al. 2019; Jamaica, Dustan & Lang 2019; Puerto Rico, Appeldoorn et al. 2019; Israel, Eyal et al. 2019) reveals that this group has attributes that confer ability to survive and persist under low availability of light and nutrients. Recently, a light-independent enzyme that acts in the last stages of chlorophyll biosynthesis has been identified (Vedalankar & Tripathy 2019). This enzyme is related to light absorption and energy conversion and has been maintained in some lineages of photosynthesizers, such as Sporolithales (Vedalankar & Tripathy 2019). Specific cases need to be assessed, however, understanding aspects of the organism's physiology provide valuable insights into ecological and evolutionary processes.

In the more recent clade are *S. episporum* and *Sporolithon* sp. (TVP1820), whose origin was estimated by our study at Burdigalian-Langhian (Miocene, ~17 Ma). Current species of this clade are known to Tanzania, Fiji, Panama (Pacific), Costa Rica (Atlantic), Brazil, China, and Taiwan. However, sister species (*S. episporum* and TVP1820; *S. indopacificum*, *S. erythraeum*, and *Sporolithon* sp) occur in the same ocean basin (Figure 2). The common ancestor of *S. episporum* and *Sporolithon* sp. could have occurred at same probability in the Central Indo-Pacific or Tropical Atlantic. In these scenarios, the closing of the Isthmus of Panama may be associated with the vicariant event.

Sister species in the Pacific and Atlantic as result of the Panama Isthmus closure are already well documented for reef fishes (Vawter et al. 1980; Rocha et al. 2008b; Hodge & Bellwood 2016), snapping shrimps (Knowlton & Weigt 1998), sea urchins (Lessios 1979), and asterinid starfish (Hart et al. 1997). The highest speciation rate observed in this clade is consistent with the rhodalgal facies peak in Langhian and Serravallian times (Halfar & Mutti 2005). It is suggested that the algal lithofacies expansion was due to the greater availability of nutrients resulting from increased upwelling and nutrient input into coastal systems followed by a decline in temperature (Zachos et al. 2001). After the late middle Miocene climatic optimum, 17–15 Ma, occurred a gradual cooling and resumption of ice sheets in Antarctica (Zachos et al. 2001), which favoured the expansion of coralline algae to the detriment of other reef-building organisms (Halfar & Mutti 2005).

Sporolithales origin in the Tropical Atlantic

The results obtained in this study show that *Sporolithon* species occurring in the Tropical Altantic have sister species in the Indo-Pacific and that would have reached the South Atlantic via Central Atlantic by different processes, routes, and times. Our phylogeographic analysis suggests the Caribbean as a center of dispersion, since the ancestors of *S. amadoi*, *S. yoshenigueae* and *Sporolithon* sp. currently occur in the Caribbean.

Ancient lineages, represented by *S. tenue* and *S. franciscanum*, with distribution known only for the Brazilian coast, reinforce the role of peripheral areas in generating and exporting biodiversity (Bellemain & Ricklefs 2008; Bowen et al. 2013; Harvey et al. 2020), as observed in reef fishes (Rocha et al. 2008a), macroalgae (Leliaert et al. 2018) and fissurellids (Cunha et al. 2019).

Different hypotheses have been proposed about the origin of the Brazilian marine flora, considering aspects of diversity, geological and/or oceanographic processes. Taylor (1955) considered the Caribbean a major center of dispersion in the Tropical Atlantic due to its high species richness and endemism. On the other hand, Joly (1964,1965), based on current oceanographic dynamics, proposed the Brazilian marine flora as a dispersion centre for the Caribbean via the Guyana current. However, Oliveira (1977) considered that older and species-rich sites would be centres of dispersion, so the Caribbean would be a source for the South Atlantic species. From an expanded database and using multivariate analysis, Horta et al. (2001) raised in the discussion historical oceanographic processes when considering the theory of continental drift and the formation of the South Atlantic. These authors suggested that even with the total separation of America from Africa, *ca* 100 Ma, the currents that bathed the Brazilian coast were not predominant in the North Atlantic, but directly from the South Pacific and, mainly from the Indian Ocean, potentially bringing propagules and spores that colonized the Africa and American coasts in the South Atlantic (Berggren 1980; Horta et al. 2001). As discussed above, until about 50 Ma, the Rio Grande-Walvis System prevented the circulation of large masses of water, especially the deep ones, between the north and south of the South Atlantic. Thus, the CRA until this time had the Central Atlantic as the center of dispersion, which was corroborated by our results.

Final Considerations

Our results emphasize the importance of revisiting the origin of the biodiversity of the Tropical Atlantic considering the paleo-oceanographic and biological impositions related to the different groups and their evolutionary and adaptive strategies.

Baseline studies identifying Sporolithales species are urgent. They will improve our understanding of species richness, distribution, and the role of environmental drivers and biogeographic barriers in the species distribution patterns. Furthermore, phylogeographic studies associated with model-based biogeographic reconstruction will elucidate the long history of this group. We suggest that future studies investigate different habitats, from shallow to mesophotic environments, as CRAs have revealed a high niche specificity (Twist et al. 2019; Sissini et al. submitted).

The Sporolithales are considered a tropical group, and it is expected by the center of speciation hypothesis that the high speciation rates will be found in the tropics, explaining the accumulation of species in this region. However, as already evidenced in other studies, New Zealand stands out for the high richness of extant species of CRA (Harvey et al. 2005; Broom et al. 2008; Nelson et al. 2015; Twist et al. 2019), including the Sporolithales. Recent study with birds concluded that extreme environments could increase speciation opportunities (Harvey et al. 2020), even harbouring less species richness. Even though with the advancement of knowledge of CRA flora in other marine regions, revealing different patterns of diversity, future studies should investigate the role of this region in the evolutionary history of the group.

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SUPPLEMENTARY TABLES

Table S1. List of specimens used in molecular analyses including collection data, classification in realm and province according to Spalding et al. (2007) and references.

Sequence code	Local	Realm	Province	GenBank Nº	Reference
Sporolithon indopacificum	Fiji: Nakalau	Central Indo-Pacific	Tropical Southwestern Pacific	MG051271	Maneveldt et al. (2017)
Sporolithon sp.	Philippines: Pangasinan, Bolinau, Dos Hermanos	Central Indo-Pacific	Western Coral Triangle	MT447180	Narvarte et al. (2020)
Sporolithon sp.	Philippines: Pangasinan, Bolinau, Dos Hermanos	Central Indo-Pacific	Western Coral Triangle	MT447179	Narvarte et al. (2020)
Sporolithon sp.	Philippines: Pangasinan, Bolinau, Dos Hermanos	Central Indo-Pacific	Western Coral Triangle	MT447178	Narvarte et al. (2020)
Sporolithon erythraeum	China: Hainan Sanya Luhuitou fringing reef	Central Indo-Pacific	South China Sea	MK531547	Hu; Xiao (unpub.)
Heydrichia homalopasta	New Zealand: Chatham Islands, Port Hutt	Southern Ocean	Subantarctic New Zealand	DQ167931	Haart et al. (unpub.)
Heydrichia homalopasta	New Zealand: Chatham Island, Port Hutt	Southern Ocean	Subantarctic New Zealand	DQ167934	Twist et al. (2019)
Heydrichia homalopasta	New Zealand: Chatham Island, Port Hutt	Southern Ocean	Subantarctic New Zealand	DQ167937	Twist et al. (2019)
Sporolithon sp.	Australia: Western Australia, Windy Harbour	Temperate Australasia	Southwest Australian Shelf	KY682938	Saunders (unpub.)
Sporolithon sp.	Australia: Mutton Bird I.	Temperate Australasia	East Central Australian Shelf	KY682926	Saunders (unpub.)
Sporolithon durum	New Zealand: Cable Bay, Nelson, South I	Temperate Australasia	Southern New Zealand	DQ168023	Broom et al. (2008)
Sporolithon sp. B	New Zealand: North Island, Wellington, Kapiti Island	Temperate Australasia	Southern New Zealand	DQ167999	Twist et al. (2019)
Sporolithon sp. B	New Zealand: North Island, Wellington, Kapiti Island	Temperate Australasia	Southern New Zealand	DQ167995	Twist et al. (2019)
Sporolithon sp. B	New Zealand: North Island, Wellington, Kapiti Island	Temperate Australasia	Southern New Zealand	DQ167992	Twist et al. (2019)
Sporolithon sp. B	New Zealand: North Island, Wellington, Kapiti Island	Temperate Australasia	Southern New Zealand	DQ167989	Twist et al. (2019)
Sporolithon sp. B	New Zealand: North Island, Wellington, Kapiti Island	Temperate Australasia	Southern New Zealand	DQ167987	Twist et al. (2019)
Sporolithon sp. B	New Zealand: North Island, Wellington, Kapiti Island	Temperate Australasia	Southern New Zealand	DQ167975	Twist et al. (2019)
Sporolithon sp. B	New Zealand: North Island, Wellington, Kapiti Island	Temperate Australasia	Southern New Zealand	DQ167971	Twist et al. (2019)
Sporolithon sp. B	New Zealand: North Island, Wellington, Kapiti Island	Temperate Australasia	Southern New Zealand	DQ167966	Twist et al. (2019)
Sporolithon sp. B	New Zealand: Auckland, Ritch Bitch Hole	Temperate Australasia	Northern New Zealand	DQ167962	Twist et al. (2019)
Sporolithon sp. B	New Zealand: North Island, Wellington, Kapiti Island	Temperate Australasia	Southern New Zealand	DQ167961	Twist et al. (2019)

Sporolithon sp. B	New Zealand: Hawkes Bay, Tuingara Point	Temperate Australasia	Southern New Zealand	DQ167960	Twist et al. (2019)
Sporolithon sp. A	New Zealand: Nelson, Ataata Point	Temperate Australasia	Southern New Zealand	DQ167955	Twist et al. (2019)
Sporolithon sp. A	New Zealand: South Island, Nelson, Cable Bay	Temperate Australasia	Southern New Zealand	DQ167909	Broom et al. (2008)
Sporolithon sp. A	New Zealand: Nelson, Cable Bay	Temperate Australasia	Southern New Zealand	DQ167887	Twist et al. (2019)
Sporolithon sp. B	New Zealand: South Island, Marlborough Sounds	Temperate Australasia	Southern New Zealand	DQ167875	Broom et al. (2008)
Sporolithon sp.	New Zealand, Whangaparaoa, Army Bay	Temperate Australasia	Northern New Zealand	MN539011	Zhan et al. (2020)
Sporolithon sp. B	New Zealand: Bay of Islands, North I	Temperate Australasia	Northern New Zealand	KC963421	Nelson et al. (unpub.)
Sporolithon sp. A	New Zealand: Auckland, Henderson Point	Temperate Australasia	Northern New Zealand	FJ361744	Twist et al. (2019)
Sporolithon sp. B	New Zealand: Auckland, Whau Point	Temperate Australasia	Northern New Zealand	FJ361666	Twist et al. (2019)
Sporolithon sp. A	New Zealand: Auckland, Sailors Grave	Temperate Australasia	Northern New Zealand	FJ361661	Twist et al. (2019)
Sporolithon sp. B	New Zealand: Auckland, Cavalli Passage	Temperate Australasia	Northern New Zealand	FJ361640	Twist et al. (2019)
Sporolithon sp. B	New Zealand: Auckland, Cavalli Passage	Temperate Australasia	Northern New Zealand	FJ361639	Twist et al. (2019)
Sporolithon sp. B	New Zealand: Auckland, Haraweka Is.	Temperate Australasia	Northern New Zealand	FJ361599	Twist et al. (2019)
Sporolithon sp. B	New Zealand: Auckland, Motuharakeke	Temperate Australasia	Northern New Zealand	FJ361586	Twist et al. (2019)
Sporolithon sp. B	New Zealand: Auckland, Stephenson Is.	Temperate Australasia	Northern New Zealand	FJ361584	Twist et al. (2019)
Sporolithon sp. B	New Zealand: Auckland, Wekarua Is.	Temperate Australasia	Northern New Zealand	FJ361575	Twist et al. (2019)
Sporolithon sp. B	New Zealand: Auckland, Wekarua Is.	Temperate Australasia	Northern New Zealand	FJ361573	Twist et al. (2019)
Sporolithon sp. A	New Zealand: Auckland, Okahu Channel	Temperate Australasia	Northern New Zealand	FJ361540	Twist et al. (2019)
Sporolithon sp. A	New Zealand: Auckland, Rangiatea	Temperate Australasia	Northern New Zealand	FJ361530	Twist et al. (2019)
Sporolithon sp. A	New Zealand: Auckland, Rangiatea	Temperate Australasia	Northern New Zealand	FJ361529	Twist et al. (2019)
Sporolithon sp. B	New Zealand: Auckland, Whau Point	Temperate Australasia	Northern New Zealand	FJ361527	Twist et al. (2019)
Sporolithon sp. B	New Zealand: Auckland, Okahu Is.	Temperate Australasia	Northern New Zealand	FJ361515	Twist et al. (2019)
Sporolithon sp. A	New Zealand: North Island, Raglan, Whale Bay	Temperate Australasia	Southern New Zealand	FJ361509	Farr et al. (2009)
Sporolithon sp. A	New Zealand: North Island, Bay Islands, Okahu Is,	Temperate Australasia	Northern New Zealand	FJ361495	Broom et al. (unpub.)
Sporolithon sp. A	New Zealand: North Island, Raglan, Whale Bay	Temperate Australasia	Southern New Zealand	FJ361478	Broom et al. (unpub.)
Sporolithon sp. A	New Zealand: North Island, Raglan, Whale Bay	Temperate Australasia	Southern New Zealand	FJ361476	Broom et al. (unpub.)
Sporolithon sp. A	New Zealand: North Island, Waitomo, Kiritehere Beach	Temperate Australasia	Southern New Zealand	FJ361469	Broom et al. (unpub.)

Sporolithon sp. B	New Zealand: North Island, Auckland, Taiwharanui	Temperate Australasia	Northern New Zealand	FJ361400	Broom et al. (unpub.)
Sporolithon sp. B	New Zealand: North Island, Northland, Karikari Bay	Temperate Australasia	Northern New Zealand	FJ361583	Farr et al. (2009)
Sporolithon durum	New Zealand, Whangaparaoa, Army Bay	Temperate Australasia	Northern New Zealand	KT266785	Lee et al. (2016)
Heydrichia homalopasta	New Zealand: Auckland, Rocky Bay	Temperate Australasia	Northern New Zealand	FJ361383	Twist et al. (2019)
Heydrichia homalopasta	New Zealand: Auckland, Rocky Bay	Temperate Australasia	Northern New Zealand	FJ361393	Twist et al. (2019)
Heydrichia homalopasta	New Zealand: Auckland, Matai Bay	Temperate Australasia	Northern New Zealand	FJ361438	Twist et al. (2019)
Heydrichia homalopasta	New Zealand: Auckland, Cable Bay	Temperate Australasia	Northern New Zealand	FJ361444	Twist et al. (2019)
Heydrichia homalopasta	New Zealand: Auckland, Jones Bay	Temperate Australasia	Northern New Zealand	FJ361548	Twist et al. (2019)
Heydrichia homalopasta	New Zealand: Gisborne, Lottin Point	Temperate Australasia	Northern New Zealand	MK413597	Twist et al. (2019)
Heydrichia homalopasta	New Zealand: Auckland, Cable Bay	Temperate Australasia	Northern New Zealand	MK413616	Twist et al. (2019)
Sporolithon amadoi	USA: Louisiana-Texas Border, Bright Bank, NWGMx	Temperate Northern Atlantic	Warm Temperate Northwest Atlantic	MN266237	Richards et al. (2019)
Sporolithon amadoi	USA: Louisiana-Texas Border, Bright Bank, NWGMx	Temperate Northern Atlantic	Warm Temperate Northwest Atlantic	MN266236	Richards et al. (2019)
Sporolithon amadoi	USA: offshore Louisiana, Ewing Bank, NWGMx	Temperate Northern Atlantic	Warm Temperate Northwest Atlantic	MN266235	Richards et al. (2019)
Sporolithon sp.	Taiwan: Xinwu, Taoyuan County	Temperate Northern Pacific	Warm Temperate Northwest Pacific	MH377024	Liu et al. (2018)
Sporolithon sp.	Taiwan: Xinwu, Taoyuan County	Temperate Northern Pacific	Warm Temperate Northwest Pacific	MH377023	Liu et al. (2018)
Heydrichia woelkerlingii	South Africa	Temperate Southern Africa	Agulhas	JQ917415	Merwe et al. (2015)
Heydrichia cerasina	South Africa: Cape Agulhas, Western Cape Province	Temperate Southern Africa	Agulhas	MF034551	Richards et al. (2017)
Sporolithon amadoi	Brazil: ES, São Mateus, Recifes Esquecidos	Tropical Atlantic	Tropical Southwestern Atlantic	MN434071	Richards et al. (2019)
)Sporolithon amadoi	Brazil: ES, São Mateus, Recifes Esquecidos	Tropical Atlantic	Tropical Southwestern Atlantic	MN434070	Richards et al. (2019)
Sporolithon amadoi	Brazil: ES, São Mateus, Recifes Esquecidos	Tropical Atlantic	Tropical Southwestern Atlantic	MN434069	Richards et al. (2019)
Sporolithon amadoi	Brazil: AP, Itaubal, Amazon Reefs	Tropical Atlantic	North Brazil Shelf	MN434068	Richards et al. (2019)
Sporolithon amadoi	Brazil: AP, Itaubal, Amazon Reefs	Tropical Atlantic	North Brazil Shelf	MN434067	Richards et al. (2019)

Sporolithon mesophoticum	USA: Plantagenet Bank off Bermuda	Tropical Atlantic	Tropical Northwestern Atlantic	MK159180	Richards et al. (2019)
Sporolithon sinusmexicanum	USA: Offshore Florida, Dry Tortugas Vicinity	Tropical Atlantic	Tropical Northwestern Atlantic	MF034550	Richards et al. (2018)
Sporolithon episporum	Panama: Bocas del Toro	Tropical Atlantic	Tropical Northwestern Atlantic	MF034547	Richards et al. (2017)
Sporolithon yoneshigueae	Brazil: Abrolhos continental shelf	Tropical Atlantic	Tropical Southwestern Atlantic	MF034546	Richards et al. (2017)
Sporolithon yoneshigueae	Brazil: Abrolhos continental shelf	Tropical Atlantic	Tropical Southwestern Atlantic	MF034545	Richards et al. (2017)
Sporolithon ptychoides	Brazil: Fernando de Noronha Arquipelago	Tropical Atlantic	Tropical Southwestern Atlantic	KC870927	Bahia et al. (2014)
Sporolithon ptychoides	Brazil: Fernando de Noronha Arquipelago	Tropical Atlantic	Tropical Southwestern Atlantic	KC870926	Bahia et al. (2014)
Sporolithon episporum	Costa Rica (Atlantic): Prov. Limon, Punta Cocies	Tropical Atlantic	Tropical Northwestern Atlantic	KC870925	Bahia et al. (2014)
Sporolithon tenue	Brazil: Bahia, Salvador	Tropical Atlantic	Tropical Southwestern Atlantic	KC870924	Bahia et al. (2014)
Sporolithon tenue	Brazil: Bahia, Salvador	Tropical Atlantic	Tropical Southwestern Atlantic	KC870923	Bahia et al. (2014)
Sporolithon ptychoides	Brazil: Abrolhos	Tropical Atlantic	Tropical Southwestern Atlantic	KY485313	Jesionek et al. (2016)
Sporolithon cf. *ptychoides*	Brazil: Fernando de Noronha Arquipelago	Tropical Atlantic	Tropical Southwestern Atlantic	KP142753	Adey et al. (2015)
Sporolithon franciscanum	Brazil: Bahia State, Abrolhos Continental Shelf	Tropical Atlantic	Tropical Southwestern Atlantic	KP142752	Adey et al. (2015)
Sporolithon tenue	Brazil: Bahia State, off Salvador City	Tropical Atlantic	Tropical Southwestern Atlantic	KP142751	Adey et al. (2015)
Sporolithon sp. (TVP1813)	Brazil: RN, Tourinhos	Tropical Atlantic	Tropical Southwestern Atlantic	XXXXXX	Sissini et al. (subm.)
Sporolithon sp. (TVP1820)	Brazil: RN, Rio do Fogo, Brazil	Tropical Atlantic	Tropical Southwestern Atlantic	XXXXXX	Sissini et al. (subm.)
Sporolithon sp.	Panama: Gulf of Chiriqui, near Mono Feliz	Tropical Eastern Pacific	Tropical Eastern Pacific	MF034548	Richards et al. (2017)
Sporolithon molle	Egypt: Gulf of Suez, El Tor	Western Indo-Pacific	Red Sea and Gulf of Aden	MG051272	Maneveldt et al. (2017)
Sporolithon indopacificum	Tanzania: Zanzibar Island, Chwaka Bay	Western Indo-Pacific	Western Indian Ocean	MG051270	Maneveldt et al. (2017)

Sporolithon eltorensis	Egypt: Dahab, Gulf of Aqaba	Western Indo-Pacific	Red Sea and Gulf of Aden	MF034544	Richards et al. (2017)
Sporolithon eltorensis	Egypt: El Tor, Gulf of Suez	Western Indo-Pacific	Red Sea and Gulf of Aden	MF034544	Richards et al. (2017)
Sporolithon ptychoides	Egypt: El Tor, Gulf of Suez	Western Indo-Pacific	Red Sea and Gulf of Aden	MF034542	Richards et al. (2017)
Sporolithon ptychoides	Egypt: El Tor, Gulf of Suez	Western Indo-Pacific	Red Sea and Gulf of Aden	MF034541	Richards et al. (2017)

Table S2. Occurrence of Sporolithales species in biogeographic provinces (according to Spalding et al. 2007 division). MOTU: Molecular operational taxonomic unit.

Biogeographical province	Species (MOTU)
Agulhas	*Heydrichia cerasina* (MOTU 21), *H. woelkerlingii* (MOTU 22)
East Central Australian Shelf	*Sporolithon* sp. (MOTU 13)
North Brazil Shelf	*S. amadoi* (MOTU 1)
Northern New Zealand	*Sporolithon* sp. (MOTU 8), *Sporolithon* sp. (MOTU 14), *Sporolithon* sp. (MOTU 19), *H. homalopasta* (MOTU 23)
Red Sea and Gulf of Aden	*S. molle* (MOTU 3), *S. ptychoides* (MOTU 4*), S. eltorensis* (MOTU 7)
South China Sea	*S. erythraeum* (MOTU 19)
Southern New Zealand	*Sporolithon* sp. (MOTU 8), *Sporolithon durum* (MOTU 13), *Sporolithon* sp. (MOTU 14)
Southwest Australian Shelf	*Sporolithon* sp. (MOTU 06)
Subantarctic New Zealand	*H. homalopasta* (MOTU 23)
Tropical Eastern Pacific	*Sporolithon* sp. (MOTU 16)
Tropical Northwestern Atlantic	*S. mesophoticum* (MOTU 11), *S. sinusmexicanum* (MOTU 12), *S. episporum* (MOTU 17)
Tropical Southwestern Atlantic	*S. amadoi* (MOTU 1), *S. franciscanum* (MOTU 5), *S. tenue* (MOTU 9), *S. yoneshigueae* (MOTU 10), TVP1820 (MOTU 18)
Tropical Southwestern Pacific	*S. indopacificum* (MOTU 15)
Warm Temperate Northwest Atlantic	*S. amadoi* (MOTU 1)
Warm Temperate Northwest Pacific	*Sporolithon* sp. (MOTU 20)
Western Coral Triangle	*Sporolithon* sp. (MOTU 2)
Western Indian Ocean	*S. indopacificum* (MOTU 15)

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CAPÍTULO 3

OIL SPILL RESPONSE: PROTECT RHODOLITH BEDS

(carta publicada no periódico *Science*)

formatação de acordo com as regras da revista

4. CAPÍTULO 3: OIL SPILL RESPONSE: PROTECT RHODOLITH BEDS

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In his News In Depth story “Mystery oil spill threatens marine sanctuary in Brazil” (8 November 2019, p. 672), H. Escobar highlights important ecosystems have been affected by the spill. However, he did not mention the Brazilian rhodolith beds—the most extensive, abundant, and diverse biogenic carbonate habitats in the South Atlantic (1). The oil spill severely threatens these ecosystems, which comprise a staggering 2 x 10^{11} tons of carbonatic bank (2), stretch from 5°N to 27°S along the Brazilian coast, and cover a seabed potential area of 229,000 km^2 (1).

Brazil’s rhodolith beds are recognized as oasis of diversity (3). Although they harbor species of great economic and ecological value, they remain unprotected. The oil pollution will likely cause major socio-environmental and economic losses, similar to those caused by the DeepSea Horizon incident in the Gulf of Mexico (4). The contamination will compromise the region’s food security as well as biodiversity conservation and efficient management. Moreover, the ongoing oil spill could have global consequences given the potential biogeochemical role of rhodolith beds in the oceanic carbon balance (1,5). Thus, this event must not be downplayed or concealed, as has been attempted in the case of Brazilian mining accidents (6) and Amazon deforestation and fires (7). We advocate urgent action to evaluate and mitigate the oil spill, and to remediate and restore areas on the oil slick route. Brazil must follow in the footsteps of Australia and Europe (8) and prioritize rhodolith bed conservation.

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5. CONCLUSÃO GERAL

O presente trabalho avaliou a biodiversidade de algas calcárias nos recifes brasileiros e os padrões de distribuição das espécies sob a perspectiva ecológica e evolutiva, levantando ambientes e/ou regiões prioritárias para a conservação destes organismos e dos ambientes por eles construídos. Nossos resultados ressaltam a importância de se revisitar a origem da biodiversidade no Atlântico Sul considerando imposições paleo-oceanográficas e biológicas relacionadas a diferentes grupos de organismos e suas estratégias adaptativas e evolutivas.

O uso de ferramentas moleculares associadas a métodos de delimitação de espécies se mostrou eficiente no levantamento rápido da biodiversidade, revelando 79 unidades taxonômicas operacionais moleculares (da sigla em inglês, MOTU) de algas calcárias (Corallinophycidae) presentes nos recifes brasileiros. A ecorregião Leste apresentou a maior riqueza, com o registro de 50 MOTU, seguida pelas ecorregiões Sudeste (27 MOTU) e Nordeste (23 MOTU). A ecorregião Leste destacou-se ainda pelo alto número de espécies raras (42%) e potencialmente novas espécies para a ciência, revelando-se como importante zona de transição no litoral brasileiro.

A flora coralina de ambientes mesofóticos deve ser melhor estudada e preservada, tanto pela sua importância na conectividade entre ambientes rasos e fundos, como por atuar como refúgio (BONGAERTS; SMITH, 2019) frente a distúrbios ambientais. Estes ambientes estão gravemente ameaçados pela pesca predatória (FRAGKOPOULOU et al., 2021) e mineração, e os estudos sobre a biodiversidade das algas calcárias na zona mesofótica do litoral brasileiro são escassos (p. ex., PEREIRA-FILHO et al., 2012; TÂMEGA et al., 2014; MOURA et al., 2016). Nossos resultados também evidenciaram a conectividade entre ambientes costeiros e oceânicos. No entanto, estudos filogeográficos poderão elucidar o papel das ilhas oceânicas em gerar e/ou acumular espécies e/ou linhagens, sendo este um importante aspecto para subsidiar estratégias efetivas de conservação.

Na escala ecológica, a temperatura superficial do oceano, a concentração de fosfato e a velocidade da corrente marinha foram as variáveis ambientais mais correlacionadas com as similaridades na riqueza de espécies, valores de β-diversidade e padrões de distribuição em cada ecorregião. Ao passo que as dissimilaridades entre as ecorregiões foram explicadas por diferentes combinações das variáveis avaliadas, evidenciando as particularidades e validando as divisões em ecorregiões marinhas propostas por Spalding et al. (2007) para o ASO.

Sob a perspectiva histórica, investigamos como condições climáticas passadas e paleo-oceanográficas influenciaram a diversidade e o padrão de distribuição atual das Sporolithales, com enfoque nas espécies do Atlântico Tropical. Dentre as 23 MOTU identificadas globalmente, a maior diversidade foi encontrada no Atlântico Tropical. Ao longo do tempo geológico, este grupo de algas calcárias atingiu maior riqueza de espécies em momentos planetários mais quentes, como no Óptimo Climático do Mioceno (BRAGA; BASSI, 2007).

O resultado da calibração da filogenia revelou que as espécies que ocorrem atualmente no Atlântico Tropical originaram-se em tempos diferentes, muito provavelmente o Caribe sendo o centro de dispersão, como observado em *Sporolithon amadoi*, *S. yoshenigueae* e *Sporolithon* sp. (TVP1820). Ainda, nossos resultados mostraram que a diversificação em Sporolithales foi constante no tempo e aumentou no final do Neogeno. Adaptações a condições mesofóticas (que são menos variáveis durante eventos extremos relacionados às extinções em massa) podem explicar a sobrevivência do grupo em momentos de escuridão, resfriamento e chuva ácida, como na transição do Cretáceo-Paleogeno (AGUIRRE; RIDING; BRAGA, 2007), onde 70% das espécies de algas calcárias foram extintas.

Apesar da comparação da biodiversidade entre domínios marinhos e províncias biogeográficas serem feitas com cautela, uma vez que os estudos estão concentrados em poucas regiões, como Mediterrâneo, Austrália e Nova Zelândia, nossas análises mostram que cerca de 83% das espécies de Sporolithales ocorrem em uma única província biogeográfica, sugerindo alto endemismo regional.

Nossos resultados mostram ainda que espécies de *Sporolithon* que ocorrem no Atlântico Tropical, possuem espécies irmãs no Indo-Pacífico, e que devem ter chegado via Atlântico Central por processos, rotas e tempos diferentes. Ao longo do tempo geológico, identificamos o Sistema Rio Grande–Walvis Ridge e o fechamento do Istmo do Panamá como as principais barreiras biogeográficas relacionadas aos mecanismos evolutivos das Sporolithales.

Os recifes biogênicos do Atlântico Sul Ocidental são únicos em sua composição e funcionamento. Como mencionado ao longo de todo este trabalho, as algas calcárias possuem papel ecológico fundamental, formando a estrutura tridimensional que servirá de abrigo para uma vasta diversidade de fauna e flora, favorecendo desde o assentamento de larvas de invertebrados, ao sequestro de carbono atmosférico (MAO et al., 2020) além de atuarem como banco de sementes de recifes ao abrigar estágios microscópicos e esporos de diferentes organismos (FREDERICQ et al., 2019). Contudo, as ameaças a esses organismos e ao ambiente por ele formados são enormes. Países da Europa e a Austrália já reconheceram a importância desses recifes coralinos algais e proibiram sua explotação ou pesca de arrasto. No Brasil, apesar do recente aumento das áreas marinhas protegidas (SOARES; LUCAS, 2018) os bancos de rodolitos ainda permanecem desprotegidos (SISSINI et al., 2020). O presente trabalho fornece novos argumentos para auxiliar o Brasil e a Organização das Nações Unidas na conservação e uso sustentável dos oceanos (objetivo de desenvolvimento sustentável 14), trazendo novos horizontes para a Década de Ciência dos Oceanos.

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