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TESE DE DOUTORADO

OS IMPACTOS DO CORAL INVASOR *TUBASTRAEA* SPP. NA PRODUÇÃO DE CARBONATO E NA COMPLEXIDADE ESTRUTURAL DE UM RECIFE BRASILEIRO: UMA ANÁLISE DO CRESCIMENTO ESQUELÉTICO, DO POTENCIAL BIOCONSTRUTOR E DA MODULAÇÃO DE VIAS TRÓFICAS

LUCAS SARMENTO NEVES DA ROCHA

SALVADOR
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Orientador: Prof. Dr. ***Ruy Kenji Papa de Kikuchi***

Tese de Doutorado apresentada ao Programa de Pós-Graduação em Geologia do Instituto de Geociências da Universidade Federal da Bahia como requisito parcial à obtenção do Título de Mestre em Geologia, Área de Concentração: Geologia Marinha, Costeira e Sedimentar.

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Aos meus pais e esposa,

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RESUMO

A bioinvasão representa um grande desafio para os ecossistemas marinhos, afetando não apenas a estrutura do habitat e a dinâmica da comunidade, mas também as funções do ecossistema como um todo. A complexidade estrutural desempenha um papel crucial na regulação da diversidade e dos níveis tróficos nos recifes de coral. No entanto, a influência específica das espécies invasoras na topografia dos recifes e nos efeitos tróficos associados ainda é pouco compreendida. Nesse estudo examinamos de forma abrangente o impacto do coral invasor *Tubastraea* nas áreas de topo do Recife de Cascos, Bahia, Brasil, abordando os impactos na estrutura da comunidade bentônica, complexidade estrutural e produção de carbonato no recife, bem como na estrutura trófica dos peixes recifais, entre 2017 e 2019. Para isso, foram utilizados vídeo-transectos, técnicas de medição de crescimento esquelético (i.e., extensão linear, densidade e calcificação), sondas digitais de profundidade e modelos tridimensionais de alta resolução das espécies de coral investigadas. Os resultados revelaram alterações nos padrões da assembleia bentônica, com um aumento na cobertura de *Tubastraea* spp. e um declínio nas algas calcárias incrustantes entre os anos avaliados. Ademais, os corais invasores exibiram uma taxa de extensão esquelética superior e densidade esquelética inferior às das espécies nativas (i.e., *Montastraea cavernosa* e *Siderastrea* sp.), sem alterações significativas na produção geral de carbonato de cálcio do recife durante o período de estudo. Também ficou evidente que os esqueletos de *Tubastraea* spp. aumentaram significativamente a rugosidade do recife, contribuindo para a complexidade do substrato em uma escala submétrica. No entanto, esse aumento não promoveu a diversidade de peixes recifais, mas evidenciou o potencial de alteração dos padrões da estrutura trófica. Especificamente, observou-se uma relação negativa entre o índice de complexidade das colônias do invasor *Tubastraea* sp. e a abundância de alguns grupos tróficos de peixes, como herbívoros e omnívoros errantes, enquanto uma relação positiva foi observada com os planctívoros. Tais resultados sugerem que modificações nos atributos do habitat induzidas por corais invasores podem impactar significativamente a dinâmica bentos-peixes, favorecendo certos grupos de peixes em detrimento de outros, o que potencialmente pode impactar e comprometer diversas funções ecossistêmicas. Este estudo ressalta a necessidade de aprofundar a compreensão dos impactos ecológicos ocasionados pelas espécies invasoras nos recifes de coral. Diante do cenário atual de mudanças globais em rápida aceleração, que intensificam os eventos de bioinvasão em escala mundial, torna-se imperativo implementar políticas regulatórias e de manejo eficazes para proteger o ambiente marinho e garantir a preservação dos serviços ecossistêmicos essenciais ao bem-estar humano.

Palavras-chave: Bioinvasão; *Tubastraea* spp.; Bentos; Crescimento esquelético; Modificação de habitat.

ABSTRACT

The invasion of non-native species poses a significant challenge to marine ecosystems, affecting habitat structure, community dynamics, and overall ecosystem functions. Structural complexity is crucial in regulating diversity and trophic levels in coral reefs. However, the specific influence of invasive species on reef topography and associated trophic effects remains poorly understood. In this study, we examined the impact of the invasive coral *Tubastraea* on the top reef areas of Cascos Reef, Bahia, Brazil, addressing its effects on benthic community structure, structural complexity, reef carbonate production, and the trophic structure of reef fish between 2017 and 2019. We utilized video transects, skeletal growth measurement techniques (linear extension, density, and calcification), digital depth probes, and high-resolution three-dimensional models of the investigated coral species. Results revealed changes in benthic assemblage patterns, characterized by increased *Tubastraea* spp. cover and a decline in encrusting calcareous algae over the years. Additionally, invasive corals exhibited higher skeletal extension rates and lower skeletal density than native species (*Montastraea cavernosa* and *Siderastrea* sp.), with no significant changes in overall reef carbonate production during the study period. Moreover, *Tubastraea* spp. skeletons significantly increased reef rugosity, contributing to substrate complexity on a submetric scale. However, this increase did not promote reef fish diversity but indicated the potential for altering trophic structure patterns. Specifically, a negative relationship was observed between the complexity index of *Tubastraea* sp. colonies and the abundance of certain fish trophic groups, such as roving herbivores and omnivores. In contrast, a positive relationship was noted with planktivores. These findings suggest that habitat attribute modifications induced by invasive corals can significantly impact benthos-fish dynamics, favoring certain fish groups over others and potentially affecting various ecosystem functions. This study underscores the importance of further understanding the ecological impacts of invasive species on coral reefs. Given the current scenario of rapidly accelerating global changes, which intensify invasion events worldwide, implementing robust regulatory and management policies becomes imperative to protect the marine environment and ensure the preservation of essential ecosystem services for human well-being.

Keywords: Biological invasions; *Tubastraea* spp.; Benthos; Coral growth; Habitat modification.

APRESENTAÇÃO

Conforme consta no regimento do Programa de Pós-Graduação em Geologia – PPGGeo da Universidade Federal da Bahia, através da Resolução nº 01/201, que "*Estabelece normas para a elaboração de Teses e Dissertações na forma de artigos científicos"*, a tese está dividida em 4 capítulos, conforme descrito a seguir:

CAPÍTULO 1 – Introdução Geral: no qual é apresentado o tema pesquisado de maneira ampla, sua relevância, a localização da área de trabalho, bem como objetivos gerais e específicos;

CAPÍTULO 2 – Artigo 1: intitulado "*Growth patterns of invasive sun corals can modulate the bioconstruction potential of coral reefs*", este artigo foi escrito em colaboração com o Dr. Ruy Kenji papa de Kikuchi, e será submetido no periódico *Marine Environmental Research*, classificado como Qualis A1 para Geociências (Fator de Impacto: 3.3);

CAPÍTULO 3 – Artigo 2: intitulado "*Effects of invasive sun corals on habitat structural complexity mediate reef trophic pathways*", este artigo foi escrito em colaboração com o Dr. Ricardo Jessouroun de Miranda, Dr. José de Anchieta C.C. Nunes e o Dr. Ruy Kenji papa de Kikuchi, e foi publicado no periódico *Marine Biology*, classificado como Qualis A1 para Geociências (Fator de Impacto: 2.4);

CAPÍTULO 4 – Conclusões: neste capítulo, são apresentadas as considerações finais sobre o trabalho desenvolvido, seguidas de sugestões para novas pesquisas na área.

A justificativa de participação dos coautores no Artigo 2 está descrita no **APÊNDICE A**. Os **APÊNDICES B** e **C** contêm o Material Suplementar referente aos Artigos 1 e 2, respectivamente.

As regras de formatação dos Artigo 1 e 2 são descritas nos **ANEXOS A** e **B**, respectivamente. O comprovante de submissão do Artigo 1 está incluído no **ANEXO C**, enquanto o comprovante de aceite e publicação do Artigo 2 está apresentado no **ANEXO D**.

SUMÁRIO

CAPÍTULO 1
INTRODUÇÃO GERAL

A globalização das economias, do comércio e do turismo tem impulsionado um aumento contínuo na introdução de espécies invasoras nos ecossistemas marinhos, principalmente associadas ao transporte marítimo e à aquicultura (Ruiz et al. 2000; Kolar 2002; Seebens et al. 2013, 2021). Essa crescente introdução representa uma séria ameaça à biodiversidade global, desencadeando impactos ambientais, sociais e econômicos de grande magnitude, amplamente documentados pelo mundo (Ruiz et al. 1997; Grosholz 2002; Bax et al. 2003; Molnar et al. 2008; Carlton 2009).

Espécies de corais invasores, como o coral-sol (*Tubastraea* spp.), oriundas do Indo-Pacífico (Cairns 1994), foram introduzidas no Oceano Atlântico Sul na década de 1980 (Castro and Pires 2001; Paula and Creed 2004). Esses corais possuem características favoráveis à sua proliferação, como maturidade precoce, reprodução sexual e assexuada (Glynn et al. 2008a; Paula et al. 2014a; Capel et al. 2017), altas taxas de fertilidade (Paula et al. 2014a), crescimento rápido, alto potencial competitivo (Wellington and Trench 1985a), e capacidade de colonizar vários habitats, substratos e orientações (Creed and Paula 2007; Mizrahi et al. 2014; Miranda et al. 2016a; Mizrahi 2017). Diferentemente de corais zooxantelados, esses corais azooxantelados não dependem da luz para sobreviver (Wellington and Trench 1985a; Cairns 1994; Creed and Paula 2007; Paula et al. 2014a), o que aumenta sua capacidade de ocupação e contribui para seu sucesso como organismo oportunista. Após sua introdução, o coral-sol expandiu sua distribuição de forma descontínua ao longo de 3.850 km da costa brasileira, desde o estado do Ceará (Soares et al. 2018, 2020) até Santa Catarina (Capel et al. 2020), habitando costões rochosos, recifes e substratos artificiais (Castro and Pires 2001; Paula and Creed 2004; Creed 2006; Creed et al. 2017b). Sua rápida e descontrolada disseminação merece atenção (Silva et al. 2014), pois tem capacidade de impactar as interações tróficas (Miranda et al. 2018a; Silva et al. 2019; Neves da Rocha et al. 2024), modificar comunidades (Lages et al. 2011), danificar espécies endêmicas (Creed 2006; Santos et al. 2013a; Barbosa et al. 2019) e reduzir o recrutamento de corais nativos (Miranda et al. 2018b).

Espécies do gênero *Tubastraea* são geralmente classificadas como corais ahermatípicos (não construtores de recifes) (Wells 1993), embora existam estudos que demonstrem seu potencial como construtores de recifes (Schuhmacher 1984). Nesse sentido, Schuhmacher e Zibrowius (1985) propuseram uma revisão terminológica que considera a capacidade de *Tubastraea* de formar uma estrutura carbonática tridimensional, contribuindo significativamente para a topografia dos recifes. Recentemente, Capasso et al. (2022) demonstraram que, em nível molecular, a *Tubastraea* possui componentes específicos em seu "kit de calcificação" que conferem a esses corais uma vantagem em estratégias de calcificação. Assim, a estrutura da colônia alcançada pelo brotamento extra-tentacular (Cairns 1994) e a alta taxa de crescimento sugerem que as espécies de *Tubastraea*, em condições específicas, podem desempenhar a função de um coral construtor no arranjo tridimensional do recife. Quantificar a contribuição de cada espécie de coral para a topografia do substrato do recife possibilita avaliar com precisão possíveis mudanças estruturais (Bozec et al. 2015) e implicações na fauna associada. Considerando a importância econômica e ecológica dos recifes (Kleypas et al. 2001), os corais escleractínios hermatípicos (i.e., construtores de recifes, geralmente associados a dinoflagelados simbióticos conhecidos como zooxantelas) (LaJeunesse et al. 2018) têm sido o principal foco de pesquisa acadêmica relacionada à calcificação ao longo dos anos. Por outro lado, os corais escleractínios ahermatípicos carecem de estudos sobre seus parâmetros de crescimento e, até o momento, permanecem sub-representados neste campo do conhecimento.

Desde a descoberta da formação de bandas de densidade em corais maciços por Knutson et al. (1972), inúmeros estudos de crescimento têm sido conduzidos com diferentes espécies de corais em regiões ao redor do mundo, particularmente nos recifes do Caribe (Stearn et al. 1977; Gladfelter et al. 1978; Huston 1985; Hughes 1987; Crabbe 2010) e na Austrália (Harriott 1998, 1999; Lough and Barnes 2000; Browne 2012). Estes estudos geralmente têm como objetivo avaliar pelo menos um dos três componentes essenciais para medir o crescimento esquelético em corais escleractínios: taxa de extensão linear, definida como a distância da linha de base até a extremidade externa do novo esqueleto precipitado durante um intervalo de tempo específico (Smith et al. 2007; Manzello 2010; Morgan and Kench 2012); densidade esquelética, calculada como a massa dividida pelo volume total envolvido (Bucher et al. 1998; Smith et al. 2007); e taxa de calcificação líquida, resultante do produto da taxa de extensão linear e da densidade esquelética (Dodge and Brass 1984; Morgan and Kench 2012; Courtney et al. 2021). A densidade esquelética é tipicamente inversamente relacionada à taxa de extensão linear para muitas espécies de coral (Lough and Barnes 2000). No Brasil, Leão (1982) realizou o primeiro estudo de crescimento anual de *Mussismilia braziliensis* com base no bandamento de densidade. Trinta anos mais tarde, outro estudo de Kikuchi et al. (2013), mostrou, através da variabilidade da densidade e da extensão dessas bandas, a sazonalidade do crescimento dessa espécie, além de apontar a relação dessas variáveis (i.e., densidade e extensão linear) com a temperatura da água do mar. Apesar dos esforços científicos, as estimativas de crescimento para outros grupos morfológicos permanecem escassas, visto que o foco da pesquisa ao longo do tempo quase sempre esteve associado aos corais com formas de crescimento maciças e colunares. Neste contexto, informações sobre os parâmetros de crescimento das espécies do gênero *Tubastraea* no Oceano Atlântico Sul são praticamente inexistentes, limitadas a um único estudo que relatou taxas médias de crescimento linear de 1,01 e 0,92 cm ano^{-1} para *Tubastraea coccinea* e *Tubastraea tagusensis*, respectivamente, na Baía da Ilha Grande (Rio de Janeiro, Brasil) (De Paula 2007).

O crescimento coralíneo se manifesta em uma variedade de formas individuais (e.g., maciças, ramificadas, tabulares, incrustantes, colunares, de vida livre). No entanto, a extensão esquelética e a calcificação das assembleias de corais construtores de recifes exercem controle coletivo sobre a produtividade e a geomorfologia dos complexos recifais (Vecsei 2004; Morgan and Kench 2012). Vários métodos são comumente empregados para estimar a produção de carbonato nos recifes, fornecendo estimativas de produção agregada em escalas local e global. Estes incluem técnicas hidroquímicas baseadas em mudanças na química da água, abordagens baseadas em censo utilizando dados de cobertura bentônica e taxas de extensão/produção, estimativas geológicas de acumulações líquidas de carbonato em recifes individuais e técnicas de modelagem numérica focadas na acresção líquida nos recifes (Vecsei 2004). As taxas de produtividade derivadas de medições hidroquímicas frequentemente representam a produção de carbonato para comunidades de recifes inteiras, sem distinguir as contribuições relativas de diferentes tipos de produtores. Em contraste, métodos de censo permitem determinar as contribuições relativas de diferentes grupos biológicos para a produção líquida de carbonato de um recife (Perry et al. 2012) e realizar análises detalhadas em escalas sub-recifais (Harney and Fletcher 2003).

Entre os métodos de censo, a metodologia *ReefBudget* oferece um protocolo prático que quantifica as contribuições relativas de diferentes grupos de organismos produtores e erodedores de carbonato, gerando uma métrica final que reflete a produção líquida de carbonato impulsionada por processos biológicos (kg $CaCO_3$ m^{-2} ano^{-1}). As taxas de produção e erosão são determinadas a partir de dados de cobertura e abundância dos organismos medidos *in situ*, integrados com taxas de extensão, produção ou erosão extraídas da literatura. O protocolo e as planilhas de entrada de dados disponíveis online (http://www.exeter.ac.uk/geography/reefbudget) têm foco na região do Caribe, mas o método possui potencial de adaptação para aplicação em locais do Indo-Pacífico (Perry et al. 2012), e em outros recifes do mundo. Até o momento, não foram identificados estudos que utilizem especificamente a metodologia *ReefBudget* para quantificar a produção de carbonato em recifes brasileiros. No entanto, utilizando um método similar adaptado de Done (1995), Freitas et al. (2019) calcularam o índice Valor de Bioconstrução (*Bioconstruction Value*, Bv) para diferentes espécies de corais maciços (*Mussismilia braziliensis*, *Mussismilia hispida*, *Mussismilia harttii*, *Montastraea cavernosa* e *Siderastrea stellata*) em recifes da região de Abrolhos, no sul da Bahia, Brasil. Esse índice é definido como um parâmetro capaz de descrever a estrutura e complexidade do recife, considerando a abundância de organismos de diferentes idades. Fundamentado na ideia de que o processo de sucessão nos recifes é uma força motriz da bioconstrução, o índice pressupõe que a idade e o tamanho das colônias refletem diretamente o desenvolvimento da estrutura calcária dos recifes (Done 1995).

A complexidade estrutural é um atributo crítico no controle das interações ecológicas (e.g., relações intra e interespecíficas) e na provisão de serviços ecossistêmicos (e.g., disponibilidade de áreas de nicho em diferentes escalas) fornecidos pelos recifes de coral (Graham 2014). Os corais construtores de recifes criam estruturas físicas complexas que sustentam altos níveis de biodiversidade associada (Graham and Nash 2013a; Rogers et al. 2014). Relações positivas entre a complexidade do habitat e a abundância de peixes sugerem que a topografia do recife é essencial na estruturação das assembleias de peixes (Hixon and Beets 1993; McCormick 1994b). No entanto, outros estudos não encontraram essa mesma relação (Ault and Johnson 1998; Dustan et al. 2013). Outros grupos de organismos também podem contribuir significativamente para a tridimensionalidade do espaço recifal, como algas coralinas (Leão et al. 2003; Hamylton et al.

2017), macroalgas (Levin and Hay 1996), corais moles (Wilson et al. 2007; Epstein and Kingsford 2019) e esponjas (Diaz and Rützler 2001), assim como as matrizes mortas subjacentes formadas pelos restos de carbonato desses organismos posteriormente incorporados ao recife, e a história geológica do próprio local (Kleypas et al. 2001). Por outro lado, perturbações físicas (e.g., tempestades tropicais) e biológicas (e.g., branqueamento de corais e doenças) quase sempre produzem perda ou modificação da complexidade do habitat (Wilson et al. 2006; Alvarez-Filip et al. 2011b). Apesar da importância da complexidade estrutural para os ecossistemas de recifes, a influência de espécies invasoras sobre eles ainda é pouco estudada.

Sem inovação recente nos métodos de controle, espera-se que a dispersão do coral invasor *Tubastraea* no Oceano Atlântico Sul continue ao longo do tempo (Capel et al. 2019; Coelho et al. 2022; Crivellaro et al. 2022; Calado et al. 2023). Apesar dos avanços significativos na compreensão de várias questões científicas relacionadas ao coral-sol no Brasil, como as estratégias de reprodução (Glynn et al. 2008a; Paula et al. 2014a), sua dispersão e ocupação geográfica ao longo do tempo (Sampaio et al. 2012; Carlos-Júnior et al. 2015; Creed et al. 2017b), interações ecológicas com espécies nativas de corais (Santos et al. 2013a; Miranda et al. 2016a, 2018b) e peixes recifais (Miranda et al. 2018a), pouco se sabe sobre os padrões de crescimento deste coral invasor, e como o aumento de sua população estão relacionados com a produção de carbonato e a conformação geométrica e estrutural dos recifes. Neste contexto, estudos de monitoramento contínuo de sua expansão nos recifes ao largo da costa brasileira são cruciais para uma melhor compreensão da história de vida deste gênero e de sua ecologia populacional.

Os métodos de controle empregados contra o coral invasor *Tubastraea* spp. consistem predominantemente na remoção mecânica manual realizada por mergulhadores, utilizando formão e martelo (Creed et al. 2017a). Iniciativas baseadas nesses métodos foram implementadas localmente por agências governamentais ambientais, organizações não governamentais, pesquisadores e voluntários no Brasil e têm se mostrado eficazes na redução da cobertura do coral-sol (De Paula et al. 2017). No entanto, os estudos realizados por Luz et al. (2018) indicam que esse organismo apresenta altas taxas de regeneração, podendo voltar a crescer a partir de tecido remanescente que não é completamente removido do substrato, o que compromete a eficácia do controle. Atualmente, em casos específicos, também tem sido empregadas ferramentas elétricas para facilitar e acelerar o processo de remoção, a exemplo do uso de martelos de impacto e escovas rotativas (Carboni et al. 2024). Apesar do Ministério do Meio Ambiente ter publicado, em 2018, um Plano Nacional para Prevenção, Controle e Monitoramento (PNPCM) de *Tubastraea* spp. (MMA 2018), até o momento, nenhuma ação de controle foi implementada em escala nacional (Crivellaro et al. 2022).

A área de estudo compreendeu o Recife Cascos (13°07′46″S, 38°38′31″W), situado na porção externa da Baía de Todos os Santos (BTS), costa leste do Brasil, Atlântico Sudoeste. O sistema recifal desta área compreende diversos *patches* irregularmente espaçados, variando em forma e tamanho, e cercados por areia calcária e terrígena. Tipicamente, as áreas de topo dos *patches* variam de 5 a 7 metros de diâmetro, com raros casos ultrapassando 10 metros (Neves da Rocha et al. 2024). Essas estruturas se estendem horizontalmente por até 100 metros de comprimento e 13 metros de altura, com uma profundidade de base alcançando 21 metros (Miranda et al. 2016a, 2018a). A comunidade bentônica inclui algas calcárias incrustantes e ramificadas, macroalgas, esponjas, ascídias, briozoários, octocorais e corais escleractínios. As espécies nativas de corais escleractínios são *Montastraea cavernosa*, *Madracis decactis*, *Phyllangia americana*, *Astrangia* spp., *Mussismilia hispida*, *Siderastrea* sp. e *Meandrina braziliensis*, bem como o hidróide calcário *Millepora alcicornis* (Neves da Rocha et al. 2024). Importante destacar que o Recife dos Cascos se encontra nas proximidades da borda limítrofe da Área de Preservação Ambiental (APA) da BTS, área protegida a qual equivale à categoria V da *International Union for Conservation of Nature* (Cruz et al. 2009).

Tubastraea tagusensis e *Tubastraea coccinea* foram relatados pela primeira vez no Atlântico Sudoeste no início da década de 1980 (Castro and Pires 2001; Creed et al. 2017b). Espécimes com coralitos plocóides geralmente são descritos como *T. coccinea*, e espécimes com coralitos dendróides são descritos como *T. tagusensis*. No entanto, Bastos et al. (2022) encontraram, por meio de estudos genéticos e morfológicos, dois morfotipos da espécie plocóide que ainda classificam como *T. coccinea* e um terceiro morfotipo com coralitos dendróides, não representativo de *T. tagusensis* apesar de descrições anteriores descrevendo *T. tagusensis* no Brasil. Assim, o presente trabalho considerou duas espécies invasoras de coral-sol: *T. coccinea* (morfotipos plocóides) e *Tubastraea* sp. (morfotipo dendróide). Relatos da presença de *Tubastraea* spp. no Recife dos Cascos e em outros locais na costa leste do Brasil tem sido observado desde 2011 (Sampaio et al. 2012). Estudos recentes de Miranda et al. (2016, 2018a) no próprio Recife dos Cascos descreveram os padrões de linha de base desta população invasora, inicialmente como aglomerados de colônias em áreas relativamente pequenas, seguido por uma expansão populacional em termos de aumento na cobertura percentual ao longo do recife três anos após a primeira avaliação ter sido realizada.

O presente trabalho teve como objetivo realizar uma estimativa quantitativa, baseada em censo, da produção de carbonato de cálcio das espécies de coral invasoras (*Tubastraea* spp.) e nativas (*Montastraea cavernosa* e *Siderastrea* sp.) em um recife brasileiro ao longo de dois anos, explorando diferenças intraespecíficas, interespecíficas e temporais. Esse mesmo trabalho também avaliou a influência do coral invasor *Tubastraea* spp. em diferentes escalas de complexidade estrutural nas regiões de topo do recife, examinando as relações entre a complexidade individual das colônias de coral e a rugosidade do substrato. Os objetivos específicos foram os seguintes:

- CAPÍTULO 2 – Artigo 1: (i) verificar diferenças temporais na cobertura bentônica em um recife invadido por *Tubastraea* spp.; (ii) quantificar e comparar parâmetros de crescimento (i.e., extensão linear esquelética, densidade esquelética e taxa de calcificação) das espécies de coral avaliadas; (iii) estimar a taxa anual de produção de carbonato de cálcio do recife em diferentes anos avaliados (i.e., 2017 e 2019);
- CAPÍTULO 3 – Artigo 2: (iv) investigar a influência do invasor *Tubastraea* spp. na produção geral de carbonato de cálcio do recife; (v) e investigar as implicações associadas a possíveis mudanças na complexidade estrutural para os grupos tróficos de peixes recifais.

Este trabalho fornece as primeiras estimativas do crescimento esquelético e do potencial de produção de carbonato do coral invasor *Tubastraea* em um recife natural no Oceano Atlântico Sul. Além disso, revela como a expansão populacional deste gênero pode modular o potencial de construção, a complexidade estrutural e as vias tróficas dos recifes de coral ao longo do tempo, cujos impactos diretos ainda são pouco compreendidos.

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CAPÍTULO 2

ARTIGO 1

Submetido para: *Marine Environmental Research*

Growth patterns of invasive sun corals can modulate the bioconstruction potential of coral reefs

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Abstract

The invasion of non-native species poses significant challenges to marine ecosystems, with implications for habitat structure and community dynamics. In this study, we investigated the impact of invasive corals on benthic community structure and coral carbonate production in Cascos Reef, Brazil. We assessed changes in benthic cover and coral growth parameters between 2017 and 2019 using video transects and different skeletal growth techniques. Our results show significant differences in benthic assemblage patterns, with an increase in *Tubastraea* spp. cover and a decrease in crustose coralline algae. Additionally, invasive corals exhibited higher skeletal extension rates and similar bulk skeletal density than native species. Despite these differences, there were no significant changes in overall coral carbonate production of the Cascos Reef over the study period. These findings underscore the importance of understanding the ecological implications of invasive species in coral reef ecosystems for effective management and conservation strategies.

Keywords: Introduced species; Benthos; Coral growth; Carbonate production; Reefs; Marine ecosystems; Todos os Santos Bay; South Atlantic.

Highlights

- Invasive corals like *Tubastraea* spp. alter benthic structure in Cascos Reef, Brazil.
- Benthic analysis reveals shifts: more invasive coral, less crustose algae.
- Invasive corals show higher extension rates and lower density than natives.
- Despite growth differences, overall coral carbonate production remains stable.
- Understanding invasive species impacts is crucial for coral reef conservation.

1. Introduction

The globalization of economies, trade, and tourism has led to a continuous increase in species translocated and introduced into marine ecosystems (Ruiz et al. 1997; Kolar 2002; Seebens et al. 2013, 2021). These introductions, primarily associated with shipping and aquaculture, pose a severe threat to global biodiversity, causing significant environmental, social, and economic impacts (Ruiz et al. 1997; Grosholz 2002; Bax et al. 2003; Molnar et al. 2008; Carlton 2009).

Invasive coral species, such as the sun coral (*Tubastraea* spp.), originally from the Indo-Pacific (Cairns 1994), were introduced into the South Atlantic Ocean in the 1980s (Castro and Pires 2001; Paula and Creed 2004). These corals have demonstrated characteristics that favor their proliferation, such as early maturity, sexual and asexual reproduction (Glynn et al. 2008a; Paula et al. 2014b; Capel et al. 2017), high fertility rates (Paula et al. 2014b), rapid growth, high competitive potential (Wellington and Trench 1985b), and the ability to colonize various habitats, substrates, and orientations (Creed and Paula 2007; Mizrahi et al. 2014; Miranda et al. 2016b; Mizrahi 2017). Unlike their zooxanthellate counterparts, these azooxanthellate corals do not depend on light to survive (Wellington and Trench 1985b; Cairns 1994; Creed and Paula 2007; Paula et al. 2014b), which enhances their occupancy capacity and contributes to their success as opportunistic organisms. After their introduction, the sun coral expanded its distribution discontinuously along 3850 km of the Brazilian coast, from the state of Ceará (Soares et al. 2018, 2020) to Santa Catarina (Capel et al. 2020), inhabiting rocky shores, reefs, and artificial substrates (Castro and Pires 2001; Paula and Creed 2004; Creed 2006; Capel et al. 2017). Its rapid and uncontrolled spread is concerning (Silva et al. 2014), as it impacts trophic interactions (Miranda et al. 2018a; Silva et al. 2019; Neves da Rocha et al. 2024), modifies communities (Lages et al. 2011), damages endemic species (Creed 2006; Santos et al. 2013a; Barbosa et al. 2019), and reduces the recruitment of native corals (Miranda et al. 2018b).

Tubastraea species are commonly categorized as ahermatypic (Wells 1993); however, evidence suggests their potential role as reef builders (Schuhmacher 1984). In this context, Schuhmacher and Zibrowius (1985) proposed a terminological revision acknowledging the ability of *Tubastraea* to form three-dimensional carbonate structures and significantly contribute to reef carbonate production. Recently, Capasso et al. (2022) demonstrated that at the molecular level, *Tubastraea* has specific components in its "calcification toolkit" that give these corals an advantage in calcification strategies. Thus, despite the reported deleterious effects intrinsic to an invasive organism (Creed 2006; Santos et al. 2013a; Miranda et al. 2018a, b; Barbosa et al. 2019), the colony structure achieved by extra-tentacular budding (Cairns 1994) and the high growth rate of *Tubastraea* species (Wellington and Trench 1985b) suggest that this coral may significantly contribute to the formation of the three-dimensional structure (Neves da Rocha et al. 2024) and carbonate production of a reef (Schuhmacher and Zibrowius 1985). Considering reefs' economic and ecological importance (Kleypas et al. 2001), hermatypic scleractinian corals (i.e., reef builders, typically associated with symbiotic dinoflagellates known as zooxanthellae) (LaJeunesse et al. 2018) have been the primary focus of academic research related to calcification over the years. On the other hand, ahermatypic scleractinian corals lack studies on their growth parameters and, to date, remain underrepresented in this field of knowledge (Soares et al. 2020).

Since the discovery of density band formation in massive corals by Knutson et al. (1972), numerous growth studies have been conducted with different coral species in regions worldwide, particularly in the Caribbean reefs (Stearn et al. 1977; Gladfelter et al. 1978; Huston 1985; Hughes 1987; Crabbe 2010) and Australia (Harriott 1998, 1999; Lough and Barnes 2000; Browne 2012). These studies commonly aim to assess at least one of the three essential components for measuring skeletal growth in scleractinian corals: linear extension rate, defined as the distance from the baseline to the end of the new skeleton precipitated over a specific time interval (Smith et al. 2007; Manzello 2010; Morgan and Kench 2012); skeletal density, calculated as the mass divided by the total enclosed volume (Bucher et al. 1998; Smith et al. 2007); and net calcification rate, derived from the product of linear extension rate and skeletal density (Dodge and Brass 1984; Morgan and Kench 2012; Courtney et al. 2021). Skeletal density is typically inversely related to linear extension rate across most coral species (Lough and Barnes 2000). In Brazil, the first annual growth study of Mussismilia braziliensis based on density banding was conducted by Leão (1982). Three decades later, Kikuchi et al. (2013) demonstrated the seasonal growth patterns of this species through variability in band density and extension and linked these parameters to sea surface temperature. Despite scientific endeavors, growth estimates for other morphological groups remain scarce, primarily due to the research focus on corals with massive and columnar growth forms. In this context, information regarding the growth parameters of *Tubastraea* species in the South Atlantic Ocean is virtually absent, limited to a solitary study that reported average linear growth rates of 1.01 and 0.92 cm year^{-1} for *Tubastraea coccinea* and *Tubastraea tagusensis*, respectively, in Baía da Ilha Grande (Rio de Janeiro, Brazil) (De Paula 2007).

Coral growth manifests in various forms (e.g., massive, branching, plating, encrusting, columnar, free-living). Nevertheless, reef-building coral assemblages' skeletal extent and calcification exert collective control over reef complexes' ecological productivity and geomorphology (Vecsei 2004; Morgan and Kench 2012). Several methods are commonly employed to estimate carbonate production on reefs, providing aggregated production estimates at local and global scales. These include hydrochemical techniques based on changes in water chemistry, census-based approaches utilizing benthic cover data and extension/production rates, geological estimates from net carbonate accumulations on individual reefs, and numerical modeling techniques focused on net reef accretion (Vecsei 2004). Productivity rates derived from hydrochemical measurements often represent carbonate production by entire reef communities without distinguishing the relative contributions of different types of producers. In contrast, census methods allow for determining the relative contributions of different biological groups to the net carbonate production of a reef (Perry et al. 2012) and conducting detailed analyses at sub-reef scales (Harney and Fletcher 2003).

Among census methods, the *ReefBudget* methodology offers a practical protocol that quantifies the relative contributions of different carbonate-producing and eroding groups, resulting in a final metric reflecting net carbonate production driven by biological processes (kg $CaCO_3$ m^{-2} year^{-1}). Production and erosion rates are determined from in situ measurements of organism cover and abundance, integrated with extension, production, or erosion rates extracted from the literature. Although the protocol and online data entry spreadsheets are currently focused on the Caribbean, this method holds potential for adaptation and application in Indo-Pacific locations (Perry et al. 2012) and other reefs worldwide. No studies have specifically applied the *ReefBudget* methodology to quantify carbonate production on Brazilian reefs. However, using a similar method adapted from Done (1995), Freitas et al. (2019) calculated the Bioconstruction Value (Bv) index for different massive coral species (*Mussismilia braziliensis*, *Mussismilia hispida*, *Mussismilia harttii*, *Montastraea cavernosa*, and *Siderastrea stellata*) in the Abrolhos reef region, southern Bahia, Brazil. This index is defined as a parameter that describes reef structure and complexity by accounting for the abundance of organisms of different ages. Grounded in the concept that the succession process within reefs drives bioconstruction, the index presumes that colony age and size directly reflect the development of the reef's calcareous structure (Done 1995).

Without innovation in control methods, the dispersion of *Tubastraea* in the South Atlantic Ocean is expected to continue over time (Capel et al. 2019; Coelho et al. 2022; Crivellaro et al. 2022; Calado et al. 2023). In this context, studies on growth patterns that are still poorly understood and the continuous monitoring of their expansion on the reefs off the Brazilian coast are crucial for a better understanding of this genus's life history and population ecology. Thus, we conducted a quantitative census-based estimate of calcium carbonate production by invasive coral species (*Tubastraea* spp.) and native species (*Montastraea cavernosa* and *Siderastrea* sp.) on a Brazilian reef over two years and explored intra-specific, inter-specific, and temporal differences. Specifically, the objectives of this study were: (i) to verify temporal differences in benthic cover on a reef invaded by *Tubastraea* spp.; (ii) to quantify and compare growth parameters (i.e., skeletal linear extension, bulk skeletal density, and calcification rate) of coral species evaluated on this reef; (iii) to estimate the annual calcium carbonate production rate of the reef in different years assessed (i.e., 2017 and 2019); and (iv) to investigate the influence of the invasive coral *Tubastraea* spp. on the overall calcium carbonate production of the reef. This article provides the first growth estimates through skeletal measurements and carbonate production potential of the invader *Tubastraea* on a natural reef in the South Atlantic Ocean. It reveals how the population expansion of this genus may modulate the reef-building potential of coral reefs over time, the direct impacts of which are still not fully understood.

2. Material and methods

2.1. Study area

The study was conducted from February 2017 to March 2019 in Cascos Reef (CR; 13°07′46″S, 38°38′31″W), situated within the outer portion of Todos os Santos Bay (TSB) on the east coast of Brazil, Southwest Atlantic (Fig. 1A). The reef system in this area comprises numerous irregularly spaced patch reefs, varying in shape and size, and surrounded by calcareous and terrigenous sand (Lessa and Dias 2009). Typically, reef top areas range from 5 to 7 meters in diameter, with rare instances exceeding 10 meters (Neves da Rocha et al. 2024). These reef structures extend horizontally up to 100 meters long and 13 meters high, with a base depth reaching 21 meters (Miranda et al., 2018a, 2016). It is important to highlight that the CR is located near the Baía de Todos os Santos Environmental

Protection Area (APA-BTS) boundary, a protected area classified as category V by the International Union for Conservation of Nature (Cruz et al. 2009).

The benthic community includes encrusting and branched coralline algae, macroalgae, sponges, ascidians, bryozoans, octocorals, and scleractinian corals. Native scleractinian coral species include *Montastraea cavernosa*, *Madracis decactis*, *Phyllangia americana*, *Astrangia* spp., *Mussismilia hispida*, *Siderastrea* sp., and *Meandrina braziliensis*, as well as the calcareous hydroids *Millepora alcicornis* (Neves da Rocha et al. 2024).

Tubastraea tagusensis and *Tubastraea coccinea* were first reported in the Southwestern Atlantic in the early 1980s (Castro and Pires 2001; Creed et al. 2017a). Specimens with plocoid corallites are generally described as *T. coccinea*, and specimens with dendroid corallites are described as *T. tagusensis*. However, Bastos et al. (2022) found through genetic and morphological studies that there are two morphotypes of the plocoid species that they still classify as *T. coccinea* and a third morphotype with dendroid corallites, not representative of *T. tagusensis* despite earlier descriptions describing *T. tagusensis* in Brazil. Thus, this study considered two species of invasive sun coral: *T. coccinea* (plocoid morphotypes) and *Tubastraea* sp. (dendroid morphotype).

Tubastraea spp. has been observed in CR and other regional sites since 2011 (Sampaio et al., 2012). Recent studies by Miranda et al. (2016, 2018a) in CR described the baseline patterns of this invasive population, initially observed as clumped colony patches in relatively small areas, followed by population expansion with an increasing percent cover along the reef three years after the initial assessment.

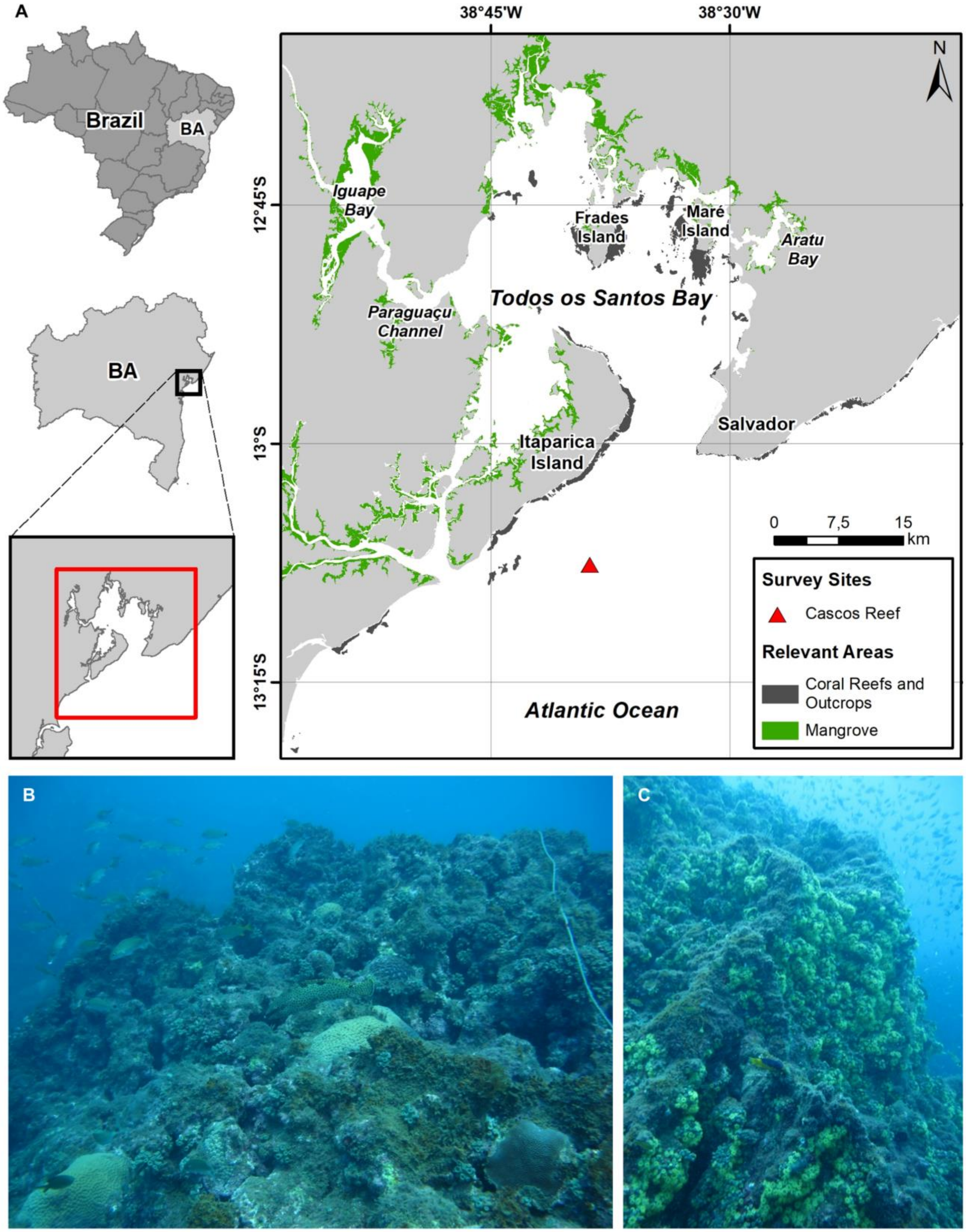

Fig. 1 Study region. **A** Map showing the location of Cascos Reef outside the Todos os Santos Bay (Bahia, Brazil); **B** and **C** show a studied reef with a high cover of the invasive coral *Tubastraea* spp.

2.2. Benthic cover

Benthic percentage cover was estimated using video transects (VTs), recorded along fixed transects measuring 5 m in length and 60 cm in width. These transects were randomly positioned on reef tops, ensuring a minimum separation of 10 meters between each transect. The length of the transects was determined based on the specific morphology of the Cascos Reef (CR) patch reefs, as described in Section 2.1 (Study Area), to avoid data acquisition over unconsolidated substrates.

To characterize and examine potential changes in the benthic community structure (at the level of species and functional groups) of CR, two field campaigns were conducted to record VTs within the same reef area, with a two-year interval between them. The first campaign took place in February 2017, during which 26 transects were recorded, followed by a second campaign in February 2019, during which 20 transects were recorded. The depths of the transects ranged from 14.8 to 19.6 meters, with a mean depth of 17.4 ± 1.4 meters.

The analysis of VTs and the estimation of benthic cover were performed using the Video Transect Analyzer software (VTA, Version 1.0), which is available for download at https://bit.ly/VTA1installer. For further details regarding the underwater image acquisition method, the equipment used, and information on the VTA software, refer to (Neves da Rocha et al. 2024).

2.3. Staining, collection, and sample processing

12 coral colonies of different species (natives and invasives) were selected and marked with cable ties to rebar hammered into the reef. Of these, 4 colonies were *Tubastraea* sp., 4 were *T. coccinea*, 2 were *Siderastrea* sp., and 2 were *M. cavernosa*. Corals were enclosed (*in situ*) for 48 hours in 20 L transparent plastic bags containing dissolved alizarin red-S (10 g L^{-1}) attached to the base of the colonies using rubber bands to provide a permanent marker in their skeletons at the time of staining (adapted from Lamberts, 1978, 1974; Wellington and Trench, 1985; Kikuchi et al. 2013). After 24 hours of exposure, the alizarin solution was replaced with a 6-hour interval.

After one year of the staining procedure (February 16, 2017, to February 26, 2018), marked corals were collected in the reef top region of Cascos Reef at depths ranging from 16.2 m to 19.3 m. No colonies showed signs of mortality (both old and recent), bleaching (in the case of native species), and diseases in their tissue. *M. cavernosa* and *Siderastrea* sp. were chosen for analysis because they are among the primary reef builders of Brazilian reefs (Leão et al. 2003b; Dutra et al. 2006, Freitas et al. 2019).

The coral tissue was first removed in the laboratory using a high-pressure water jet (Morgan and Kench 2012). Remnant tissue, epibionts, and infaunal organisms were removed by immersing the colonies in a 10% household bleach solution for five days (Manzello 2010; Ng et al. 2019), with daily solution replacement. Skeletons of other organisms and reef substrate residues were manually removed and, when necessary, assisted by an electric rotary tool attached to a diamond milling cutter.

Clean specimens were slabbed along the plane of growth symmetry using a diamond-tipped rock saw (Manzello 2010; Morgan and Kench 2012) with water as a lubricant to reveal the alizarin mark (Smith et al. 2007). The thickness of the central slice from massive coral skeletons was standardized using an electric orbital sander and a surface guide template (*M. cavernosa*: 10 mm; *Siderastrea* sp.: 5 mm) for subsequent X-radiography to determine the linear extension rate from density bands (Knutson et al. 1972; Buddemeier et al. 1974; Hudson et al. 1976; Helmle and Dodge 2011) through the CoralXDS software (Helmle et al. 2002). The thickness of slices from invasive coral skeletons was also standardized (10 mm), even though these organisms do not form skeletal density bands. Three subsamples were made from the central slice of each coral skeleton for density measurements using the same electric rotary tool, this time attached to a diamond cutting disc.

2.4. Skeletal measurements

2.4.1. Skeletal extension

Skeletal extension rate was measured using the Alizarin staining technique (Lamberts 1978) and direct measurements (Smith et al. 2007; Manzello 2010; Morgan and Kench 2012) for *Tubastraea* sp. and *T. coccinea*. Using a stainless steel caliper, the amount of skeletal extension during the experimental period was calculated by measuring the distance between the stain's upper limit and the corallite's periphery (Fig. 2A and Fig. 2B). An average of five extension measurements for different corallite was used to determine the mean skeletal extension for each colony. The results were used to estimate each invasive species' annual mean extension rates (cm y^{-1}).

As no alizarin marker was observed in the central slice of the skeleton of *M. cavernosa* colonies, X-ray techniques and measurements of the density bands' linear extension were used to determine their skeletal extension rate, applying the same technique used by Freitas et al. (2019). Using CoralXDS software, three density band profiles were generated along the growth axis of each colony collected (Fig. 2C). The density bands were visible in the X-ray images. It was assumed that each consecutive pair of light (high density) and dark (low density) bands represented one year of skeletal growth, as observed in other massive corals from reef environments worldwide (Kikuchi et al. 2013). The boundaries of each band in CoralXDS were defined using the half-range technique, applying the same approach used by Kikuchi et al. (2013). For each density band profile, ten consecutive measurements of linear extension were performed, using the boundaries between successive light and dark bands as references, representing ten annual growth increments. Thus, considering three profiles per colony, thirty measurements were obtained per specimen. The results were used to estimate the annual mean extension rate (cm y^{-1}) of the species *M. cavernosa*.

For *Siderastrea* sp., the skeletal extension rate was estimated through alizarin staining evidence observed in the skeleton surface areas. We classified the alizarin evidence on the surface of the skeleton into three growth stages: S1, alizarin apparent on the surface, indicating no growth (linear extension = 0.00 cm y^{-1}); S2, alizarin still visible on the surface, but new skeleton addition is observable over the marking (linear extension = 0.10 cm y^{-1}); and S3, no evidence of alizarin on the surface of the skeleton, indicating higher growth (linear extension = 0.15 cm y^{-1}) (Fig. 2D). Using a stereo microscope, 15 random points were classified in each of the colonies, and the linear extension rate was calculated as the average of these points. X-ray images did not show clear density band patterns using CoralXDS, likely due to reduced or irregular colony growth. Additionally, we did not observe alizarin demarcation lines in the central slice of the skeletons of *Siderastrea* sp.

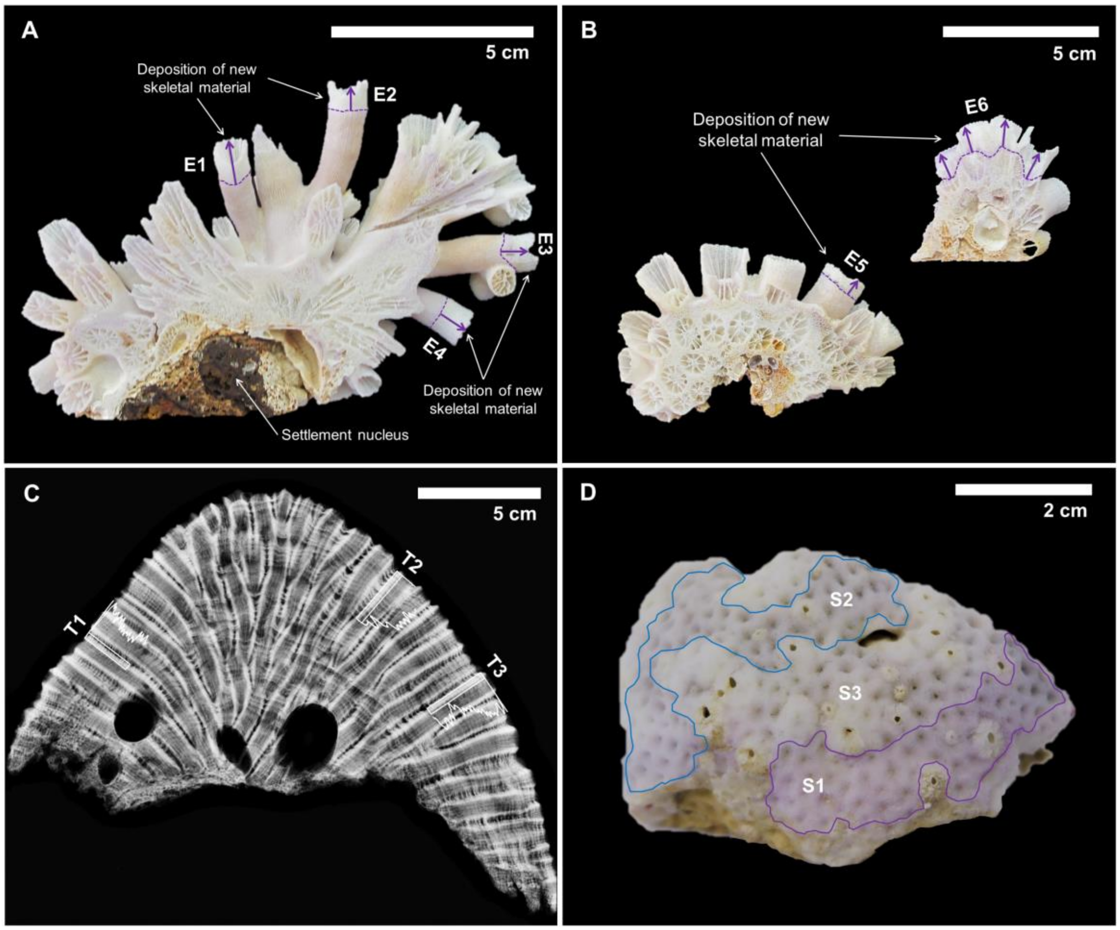

Fig. 2 A slabbed (**A**) *Tubastraea* sp. and (**B**) *Tubastraea coccinea* specimens after 12 months of growth showing the alizarin red-S stain incorporated into the skeleton (digitally highlighted) and the deposition of new skeletal material in different corallites (i.e., E1, E2, E3, E4, E5, and E6). **C** X-radiograph of a slabbed *Montastraea cavernosa* specimen, highlighting the three transects used (i.e., T1, T2, and T3) to measure the density bands' linear extension and determine their skeletal extension rate. **D** Specimen of *Siderastrea* sp. highlighting three different growth stages (i.e., S1 = no growth, S2 = 0.10 cm y^{-1}, and S3 = 0.15 cm y^{-1}) on the colony surface based on traces of alizarin red-S stain. The edge of each stage was digitally highlighted, while the internal area preserved the original coloration resulting from alizarin fixation in the coral skeleton.

2.4.2. Bulk skeletal density

Bulk skeletal density (g cm^{-3}) was determined using the Archimedes principle and was compiled from Bucher et al. (1998) and Smith et al. (2007). Subsamples (blocks) from the central slice of each coral skeleton (n = 3) were baked for 24 h at 60 °C, cooled, and then a dry weight was taken (DW_{clean}). Blocks were then dipped in molten paraffin wax at 110–115 °C to form a water-tight barrier (Smith et al. 2007). Once the samples cooled, a dry weight with wax was obtained (DW_{wax}). The buoyant weight of each waxed block was measured in distilled water at 20 °C with a specific gravity of 1.00 g cm^{-3} (BW_{wax}). The bulk density was determined by the equations presented in Table 1. All measurements were obtained with an electronic balance (Bel S2202).

2.4.3. Calcification rate

Calcification rate (g cm^{-2} y^{-1}) was calculated as a function of the skeletal extension rate and bulk density (Stearn et al. 1977; Edinger et al. 2000). However, this calculation assumes colonies have a continuous active growth surface (e.g., massive forms). Several growth morphologies (e.g., branching, digitate, plocoid, dendroid) have non-uniform carbonate deposition (i.e., do not accrete laterally and vertically at the same rate). Therefore, an adjustment coefficient (AC; 0 = no growth, 1 = continuous growth surface) was applied to each colony based on the proportion of active upward growth surfaces relative to the total colony area (Stearn et al., 1977; Hart and Kench, 2007; Carlot et al., 2020). Calcification rate was then calculated using the equations presented in Table 1. We adopted AC values of 0.4 for *Tubastraea* sp. and *T. coccinea*, and 1.0 for *Siderastrea* sp. and *M. cavernosa*, based on the morphological growth classifications and associated coefficients proposed by Morgan and Kench (2012), or those most closely resembling the growth forms of the studied species.

2.5. Carbonate production

Coral carbonate production (kg $CaCO_3$ m^{-2} y^{-1}) was calculated as a function of substrate area occupied by each coral species (i.e., mean percent cover), their skeletal extension (cm y^{-1}), and bulk density (g cm^{-3}). For this, we utilized the *ReefBudget* census-based methodology (adapted from Perry et al., 2012), which focuses on quantifying the relative contributions of different carbonate producer groups to biologically driven carbonate production. The equations in Table 1 were then applied to yield a value for coral carbonate production relative to the actual transect surface areas evaluated (see Supplementary Information, Table SI 3.1 and 3.2). The results obtained from the different transects were used to calculate the average contribution of each evaluated coral species to the carbonate production of the Cascos Reef.

Table 1 Equations used in calculating of bulk skeletal density, calcification rate, and carbonate production rate of native and invasive corals at Cascos Reef, Brazil.

Variable (units)	**Equations**	**Based or adapted from**[c]
Bulk skeletal density (g cm^{-3})	$DW_{clean} / V_{enclosed}$	Bucher et al. (1997)
	$V_{enclosed} = (DW_{wax} - BW_{wax}) \times (1.00\ g.cm^{-3})$	Smith et al. (2007)
	Where: DW_{clean} = dry weight (g) of clean skeletal material	Manzello (2010)

	$V_{enclosed}$ = enclosed volume (cm^{-3}) of waxed coral skeletons	Morgan and Kench (2012)
	DW_{wax} = dry weight (g) of waxed coral skeletons	Lionel Ng et al. (2019)
	BW_{wax} = buoyant weight (g) of waxed coral skeletons	
	1.00 g cm^{-3} = density of distilled water at 20°C	
Calcification rate ($g\ cm^{-2}\ y^{-1}$)	(SE x SD) x AC	Lough and Barnes (2000)
	Where: SE = skeletal extension rate (cm y^{-1})	Smith et al. (2007)
	SD = bulk skeletal density (g cm^{-3})	Morgan and Kench (2012)
	AC = adjustment coeff. (0-1, according to coral species)	
Carbonate production rate (kg $CaCO_3$ m^{-2} y^{-1})[a]	$\sum_i (SA_i) \times ((CR_i \times 10{,}000)/1{,}000)$	Vecsei (2004)
	$SA_i = (CC_i \times (VT_L \times VT_W))/100$	Perry et al. (2008)
	Where: SA_i = substrate area occupied (m^2) by *i*th species	N.-López et al. (2014)
	CR_i = calcification rate (g cm^{-2} y^{-1}) of the *i*th species	T.-Langarica et al. (2019)
	CC_i = % coral cover of the *i*th species in a transect	
	VT_L = video transect length (m)[b]	
	VT_W = video transect width (m)[b]	

Example for coral carbonate production rates based on data from Cascos Reef, Transect #19 (2017)

M. cavernosa: $\sum_i ((20.96 \times (5.00 \times 0.60))/100) \times ((0.26 \times 10{,}000)/1{,}000) = 1.66$ kg $CaCO_3$ m^{-2} $year^{-1}$

Siderastrea sp.: $\sum_i ((1.70 \times (5.00 \times 0.60))/100) \times ((0.17 \times 10{,}000)/1{,}000) = 0.08$ kg $CaCO_3$ m^{-2} $year^{-1}$

Tubastraea sp.: $\sum_i ((16.71 \times (5.00 \times 0.60))/100) \times ((0.26 \times 10{,}000)/1{,}000) = 1.31$ kg $CaCO_3$ m^{-2} $year^{-1}$

T. coccinea: $\sum_i ((0.00 \times (5.00 \times 0.60))/100) \times ((0.12 \times 10{,}000)/1{,}000) = 0.00$ kg $CaCO_3$ m^{-2} $year^{-1}$

Coral carbonate production for Cascos Reef, Transect #19 (2017) = 3.05 kg $CaCO_3$ m^{-2} $year^{-1}$

[a] Coral carbonate production rate was estimated considering only the species evaluated (i.e., *Montastraea cavernosa*, *Siderastrea* sp., *Tubastraea* sp., *Tubastraea coccinea*). [b] In this work, transect length (5 m) and width (0.6 m) are constants. Transect width represents the field of view of the underwater camera maintained at a constant distance from the substrate during the video transect recording. [c] The cited references are related to the calculation methods of the variables, not the equations themselves.

2.6. Statistical analysis

We employed permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001) based on Bray–Curtis dissimilarities with 999 random permutations to examine differences in benthic assemblage structure at the top of patches in Cascos Reef (CR) between 2017 and 2019. The PERMDISP routine assessed the homogeneity of multivariate dispersions from group centroids based on the resemblance measure. We utilized the similarity percentage routine (SIMPER) to compare benthic groups and species across years and identify significant changes in benthic cover. A significance level (α) of 0.05 was adopted for all analyses.

Growth parameter means (i.e., skeletal extension, bulk density, and calcification rate) and annual carbonate production (± SD) were calculated. Due to violations of normality and homoscedasticity assumptions, observed even after data transformation, differences in growth parameters (inter-specific and inter-cluster) and coral carbonate production rates (intra-specific, intra-cluster, and interannual) were evaluated using the Kruskal-Wallis and Mann-Whitney non-parametric tests. *Post-hoc* Dunn's tests were employed for all pairwise comparisons when necessary.

All analyses were performed using RStudio 2023.09.0 and R 4.3.1 software (R Development Core Team, www.r-project.org): the *vegan* package was used for PERMANOVA and the routines PERMDISP and SIMPER. Additionally, the *rstatix* package was employed for the Dunn's *post-hoc* test.

3. Results

3.1. Benthic structure patterns

Analysis of data collected between 2017 and 2019 (refer to Supplementary Information, Table SI 1.1 and 1.2) reveals the top three most prevalent benthic groups in Cascos Reef (CR) as crustose coralline algae (CCA, mean percent coverage ± standard deviation: 29.53 ± 6.84%, n = 46), turf algae (TURF, 29.40 ± 8.61%), and calcareous articulated algae (CAA, 15.80 ± 10.58%). Native corals exhibited coverage of 15.09 ± 8.62%, followed by invasive corals (8.12 ± 8.22%), macroalgae (1.14 ± 2.57%), sponges (0.58 ± 0.83%), sediment (0.28 ± 0.84%), and echinoderms (0.07 ± 0.18%) (Table 2).

Table 2 Benthic cover (%) at the top of patches in Cascos Reef. The table presents each benthic group's mean coverage (± standard deviation) based on surveys conducted in 2017 and 2019. Native corals include *Montastraea cavernosa*, *Madracis decactis*, *Mussismilia hispida*, and *Siderastrea* sp., while invasive corals include *Tubastraea coccinea* and *Tubastraea* sp.

Benthic group	Cover (%) ± SD
Native corals	15.09 ± 8.62
Invasive corals	8.12 ± 8.22
Calcareous articulated algae	15.80 ± 10.58
Crustose coralline algae	29.53 ± 6.84
Turf algae	29.40 ± 8.61
Macroalgae	1.14 ± 2.57
Sponge	0.58 ± 0.83
Echinoderms	0.07 ± 0.18
Sediment	0.28 ± 0.84

The coral cover in CR ranged from 3.08% to 41.34%, with a mean and standard deviation of 23.21 ± 9.33%. Among native hermatypic species, *M. cavernosa* dominated (11.88 ± 8.25%), followed by *Siderastrea* sp. (1.53 ± 1.51%), *M. hispida* (0.98 ± 2.00%), and *M. decatis* (0.69 ± 1.14%). Invasive ahermatypic corals were predominantly *Tubastraea* sp. (7.96 ± 8.06%) compared to *T. coccinea* (0.16 ± 0.72%) (refer Supplementary Information, Table SI 1.3).

The PERMANOVA indicated significant differences in the benthic assemblage cover pattern between 2017 and 2019 (Table 3). PERMDISP test results showed homogeneous sample dispersion across years (DF = 1, MS = 0.0020, $F = 0.6756$, $P = 0.4155$; see Supplementary Information, Table SI 1.4). SIMPER analysis highlighted significant mean cover differences between 2017 and 2019 for *Tubastraea* sp. (increase; $P = 0.0009$), CCA (decrease; $P = 0.0014$), and *M. decactis* (increase; $P = 0.0184$). However, no significant difference in coverage was observed for other benthic groups or coral species between the analyzed years ($P > 0.05$) (Fig. 3; see Supplementary Information, Table SI 1.5).

Table 3 Asymmetrical PERMANOVA analysis based on Bray–Curtis dissimilarities of benthic assemblage (percentage cover) for 2017 and 2019. The analysis was conducted with 999 permutations.

Source	**DF**	**MS**	R^2	**Pseudo-*F***	***P* (perm)**
Year	1	0.2069	0.1079	5.3229	0.001***
Residual	44	1.7100	0.8921		
Total	45	1.9169	1.0000		

*** $P < 0.001$.

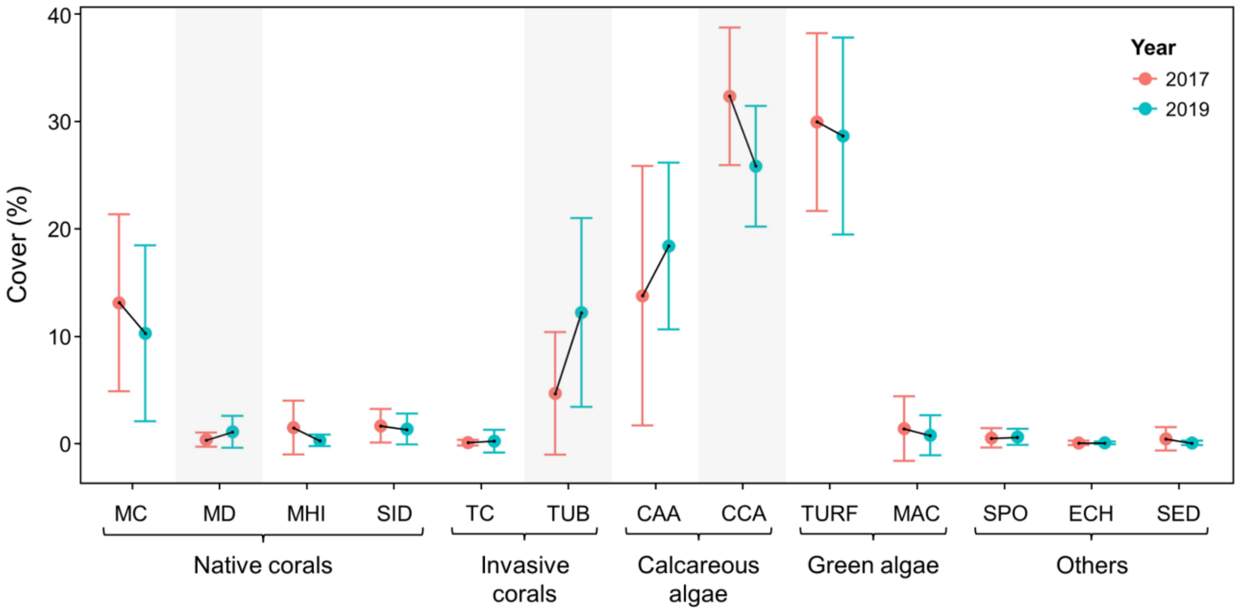

Fig. 3 Mean benthic cover (± SD) at the top of patches in Cascos Reef in 2017 (orange) and 2019 (light blue). The light gray shaded zone indicates benthic groups or species with significant differences over the years. Abbreviations: MC, *Montastraea cavernosa*; MD, *Madracis decactis*; MHI, *Mussismilia hispida*; SID, *Siderastrea* sp.; TC, *Tubastraea coccinea*; TUB, *Tubastraea* sp.; CAA, Calcareous articulated algae; CCA, Crustose coralline algae; TURF, Turf algae; MAC, Macroalgae; SPO, Sponge; ECH, Echinoderms; SED, Sediment.

3.2. Coral growth parameters

Skeletal extension varied widely among specimens ranging from 0.54 cm y^{-1} (*Tubastraea* sp.) to 0.10 cm y^{-1} (*Siderastrea* sp.). Invasive corals exhibited higher skeletal extension rates (*Tubastraea* sp., mean ± standard deviation: 0.48 ± 0.13 cm y^{-1}; *T. coccinea*: 0.27 ± 0.09 cm y^{-1}) compared to native species (*M. cavernosa*: 0.15 ± 0.04 cm y^{-1}; *Siderastrea* sp.: 0.10 ± 0.05 cm y^{-1}) (refer to Table 4 and Supplementary Information, Table SI 2.1 and SI 2.2). Comparisons between species revealed significant differences in extension rates (Kruskal-Wallis test, $\chi^2_{(3)}$ = 77.628, $P < 0.001$). *Post-hoc* analysis (pairwise Dunn's test) indicated a lack of significant difference only between *Tubastraea* sp. and *T. coccinea* ($P = 0.15$) (see Fig. 4A and Table 5).

Bulk skeletal density significantly varied among coral species ($\chi^2_{(3)}$ = 31.212, $P < 0.001$), with *T. coccinea* (1.07 ± 0.04 g cm^{-3}) showing lower density than *Tubastraea* sp. (1.39 ± 0.06 g cm^{-3}; $P = 0.03$), *Siderastrea* sp. (1.62 ± 0.07 g cm^{-3}; $P < 0.0001$), and *M. cavernosa* (1.71 ± 0.17 g cm^{-3}; $P < 0.0001$). No significant differences in skeletal density were found between *M. cavernosa* and *Siderastrea* sp. ($P = 1.00$), *Siderastrea* sp. and *Tubastraea* sp. ($P = 0.20$), and *M. cavernosa* and *Tubastraea* sp. ($P = 0.09$) (see Fig. 4B, Table 4 and Table 5).

Calcification rates also varied significantly among species ($\chi^2_{(3)}$ = 28.758, $P < 0.0001$). The annual calcification rate of *T. coccinea* (0.12 ± 0.03 g $CaCO_3$ cm^{-2} y^{-1}) was significantly lower than *Tubastraea* sp. (0.26 ± 0.03 g $CaCO_3$ cm^{-2} y^{-1}; $P < 0.0001$) and *M. cavernosa* (0.26 ± 0.02 g $CaCO_3$ cm^{-2} y^{-1}; $P < 0.001$), but not significantly different from

Siderastrea sp. (0.17 ± 0.01 g $CaCO_3$ cm^{-2} y^{-1}; $P = 0.801$). Similarly, the calcification rate of *Siderastrea* sp. did not significantly differ from *M. cavernosa* ($P = 0.156$) and *Tubastraea* sp. ($P = 0.110$) (see Fig. 4C, Table 4 and Table 5).

Table 4 Skeletal extension (cm y^{-1}), bulk skeletal density (g cm^{-3}), and calcification rate (g cm^{-2} y^{-1}) of native and invasive corals at Cascos Reef, Brazil. Coral species growth parameter values are presented as mean ± standard deviation.

Specie	***N***	***n***	**Growth morphology**	**Skeletal extension (cm y^{-1})**	**Bulk skeletal density (g cm^{-3})**	**Adjustment coefficient**	**Calcification rate (g cm^{-2} y^{-1})**
Tubastraea sp.	4	12	Dendroid	0.48 ± 0.13[a]	1.39 ± 0.06	0.4	0.26 ± 0.03
Tubastraea coccinea	4	12	Plocoid	0.27 ± 0.09[a]	1.07 ± 0.04	0.4	0.12 ± 0.03
Montastraea cavernosa	2	6	Massive	0.15 ± 0.04[b]	1.71 ± 0.17	1	0.26 ± 0.02
Siderastrea sp.	2	6	Massive	0.10 ± 0.05[c]	1.62 ± 0.07	1	0.17 ± 0.01

N represents the number of colonies, while *n* indicates subsamples taken from each coral skeleton's central slice for density measurements. [a] Estimate from alizarine staining and direct measurements; [b] X-radiography and density band measurements; [c] Alizarin staining evidences.

Table 5 Kruskal-Wallis comparison followed by Dunn's test applied to coral growth parameters (i.e., skeletal extension, bulk skeletal density, and calcification rate). In this analysis, the grouping factor is "species".

Pair-wise comparison	**Skeletal extension**			**Bulk skeletal density**			**Calcification rate**		
	Z	***P*[a]**		**Z**	***P*[a]**		**Z**	***P*[a]**	
MC-SID	-2.76	0.0346	*	-0.247	1.0000	ns	-2.23	0.1560	ns
MC-TC	3.99	0.0004	***	-4.70	<0.0001	****	-4.07	<0.001	***
MC-TUB	7.16	<0.0001	****	-2.42	0.0929	ns	-0.214	1.0000	ns
SID-TC	5.11	<0.0001	****	-4.41	<0.0001	****	-1.50	0.8010	ns
SID-TUB	7.15	<0.0001	****	-2.14	0.1960	ns	2.36	0.1100	ns
TC-TUB	2.24	0.1500	ns	2.79	0.0316	*	4.73	<0.0001	****

Abbreviations: MC, *Montastraea cavernosa*; SID, *Siderastrea* sp., TUB, *Tubastraea* sp.; TC, *Tubastraea coccinea*. [a] Adjusted for Bonferroni correction at the 95% confidence level. Significance levels: * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$), **** ($P < 0.0001$); ns indicates not significant at $P < 0.05$.

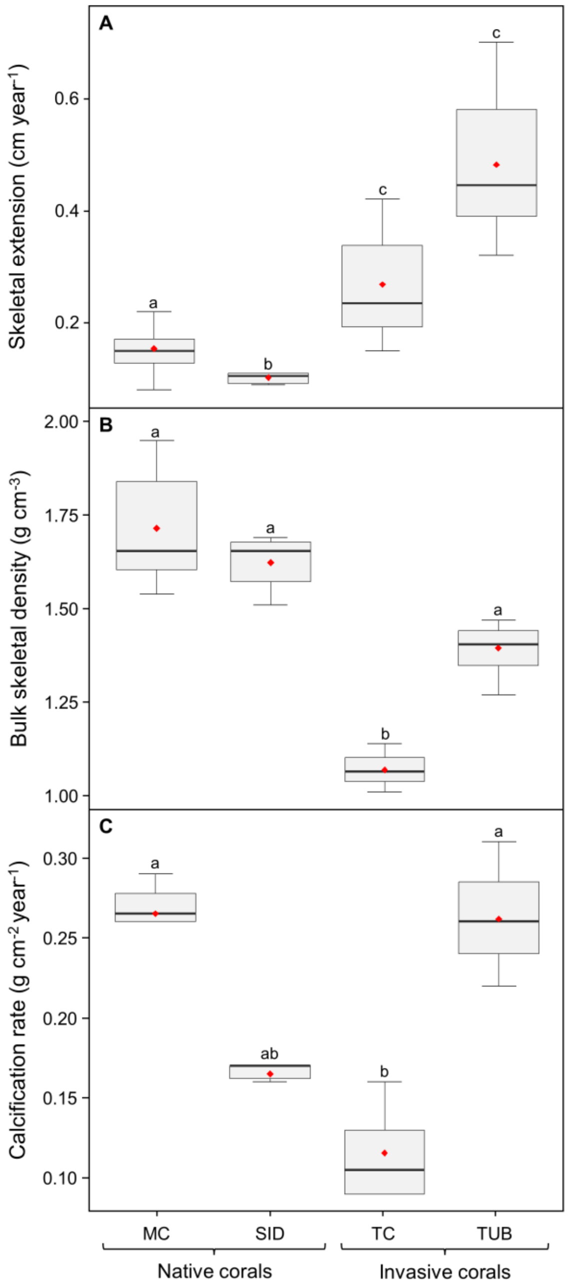

Fig. 4 Comparison of (**A**) Skeletal extension (cm y^{-1}), (**B**) bulk skeletal density (g cm^{-3}), and (**C**) calcification rate (g cm^{-2} y^{-1}) among coral species (native and invasive) in Cascos Reef, Brazil. The box plot displays the median, Q1, Q3, minimum, and maximum values, while red diamonds indicate mean values. Significant differences are denoted by letters. Abbreviations: MC, *Montastraea cavernosa*; SID, *Siderastrea* sp.; TC, *Tubastraea coccinea*; TUB, *Tubastraea* sp. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

3.3. Coral carbonate production

Coral carbonate production significantly varied among coral species (Kruskal-Wallis test, $\chi^2_{(3)} = 115.19$, $P < 0.0001$) in Cascos Reef (CR). Specifically, *T. coccinea* (mean ± standard deviation: 0.01 ± 0.02 kg $CaCO_3$ m^{-2} y^{-1}) exhibited significantly lower production compared to *Siderastrea* sp. (0.08 ± 0.07 kg $CaCO_3$ m^{-2} y^{-1}; $P = 0.0016$), *Tubastraea* sp. (0.62 ± 0.63 kg $CaCO_3$ m^{-2} y^{-1}; $P < 0.0001$), and *M. cavernosa* (0.94 ± 0.65 kg $CaCO_3$ m^{-2} y^{-1}; $P < 0.0001$). No significant difference was observed between *M. cavernosa* and *Tubastraea* sp. ($P = 0.0812$) (Fig. 5A and Table 6; see Supplementary Information, Table SI 3.3). Furthermore, a Mann-Whitney test comparing native (1.02 ± 0.66 kg $CaCO_3$ m^{-2} y^{-1}) and invasive (0.63 ± 0.64 kg $CaCO_3$ m^{-2} y^{-1}) species revealed a significant disparity in carbonate production rates ($W = 1466.5$, $P = 0.0014$) (Fig. 5B and Table 6; see Supplementary Information, Table SI 3.3).

Table 6. Carbonate production rate (kg $CaCO_3$ m^{-2} y^{-1}) of native and invasive corals at Cascos Reef, Brazil. The data reflects assessments from 2017 and 2019, with values presented as mean ± standard deviation.

Year	*N*	Carbonate production rate (kg $CaCO_3$ m^{-2} y^{-1})						
		Natives			Invaders			Total[a]
		MC	SID	Total	TUB	TC	Total	
2017	20	1.04 ± 0.65	0.08 ± 0.08	1.12 ± 0.66	0.37 ± 0.45	0.00 ± 0.01	0.37 ± 0.45	1.49 ± 0.65
2019	26	0.81 ± 0.65	0.07 ± 0.07	0.88 ± 0.65	0.96 ± 0.69	0.01 ± 0.04	0.97 ± 0.70	1.85 ± 0.87
Cascos Reef	**46**	**0.94 ± 0.65**	**0.08 ± 0.07**	**1.02 ± 0.66**	**0.62 ± 0.63**	**0.01 ± 0.02**	**0.63 ± 0.64**	**1.65 ± 0.76**

N represents the number of transects included in the analysis. [a] Site carbonate production rate (for 2017, 2019, and overall for Cascos Reef) was estimated based solely on the specified coral species (both native and invasive). Abbreviations: MC, *Montastraea cavernosa*; SID, *Siderastrea* sp., TUB, *Tubastraea* sp.; TC, *Tubastraea coccinea*.

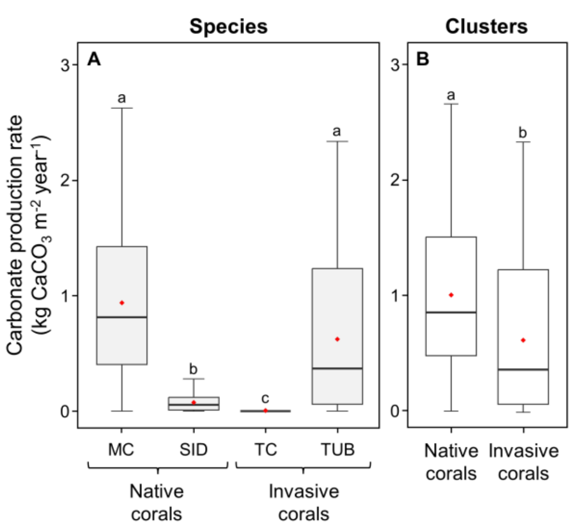

Fig. 5. Comparison of carbonate production rate (kg $CaCO_3$ m^{-2} y^{-1}) among (**A**) coral species and (**B**) clusters (i.e., native and invasive

corals). The data reflects assessments from 2017 and 2019. The box plot displays the median, Q1, Q3, minimum, and maximum values, with red diamonds indicating mean values. Letters denote significant differences. Abbreviations: MC, *Montastraea cavernosa*; SID, *Siderastrea* sp.; TC, *Tubastraea coccinea*; TUB, *Tubastraea* sp. (For color interpretation, refer to the online version of this article.)

The intra-specific comparison across different evaluated years revealed a significant difference in the carbonate production rate of *Tubastraea* sp. (Mann-Whitney test, $W = 115.5$, $P = 0.0014$) in the reef top areas of Cascos Reef (CR), showing an increase between 2017 (0.37 ± 0.45 kg $CaCO_3$ m^{-2} y^{-1}) and 2019 (0.96 ± 0.69 kg $CaCO_3$ m^{-2} y^{-1}). Regarding the native species *M. cavernosa*, the same analysis indicated a trend of reduction in carbonate production rate between 2017 (1.04 ± 0.65 kg $CaCO_3$ m^{-2} y^{-1}) and 2019 (0.81 ± 0.65 kg $CaCO_3$ m^{-2} y^{-1}); however, this difference was not found to be significant. The other investigated species (i.e., *Siderastrea* sp. and *T. coccinea*) maintained constant carbonate production rates throughout the evaluated years ($W = 320.5$, $P = 0.1836$) (Fig. 6A and Table 6; see Supplementary Information, Table SI 3.4).

The intra-cluster comparisons followed a similar pattern to the intra-specific analyses. Native corals exhibited a non-significant decreasing trend ($W = 319$, $P = 0.1948$) in carbonate production rate between 2017 (1.12 ± 0.66 kg $CaCO_3$ m^{-2} y^{-1}) and 2019 (0.88 ± 0.65 kg $CaCO_3$ m^{-2} y^{-1}) in CR, while invasive corals showed a significant increase ($W = 3430$, $P = 0.0259$) from 0.37 ± 0.45 kg $CaCO_3$ m^{-2} y^{-1} to 0.97 ± 0.70 kg $CaCO_3$ m^{-2} y^{-1} during the same period (Fig. 6B and Table 6; see Supplementary Information, Table SI 3.4).

When disregarding the comparison between species or clusters, the analysis of the overall carbonate production rate in the reef top areas of CR demonstrated that, despite the observed increasing trend between 2017 (1.49 ± 0.65 kg $CaCO_3$ m^{-2} y^{-1}) and 2019 (1.85 ± 0.87 kg $CaCO_3$ m^{-2} y^{-1}), there was no significant difference over the years ($W = 3692$, $P = 0.1847$) (Fig. 6C and Table 6; see Supplementary Information, Table SI 3.4).

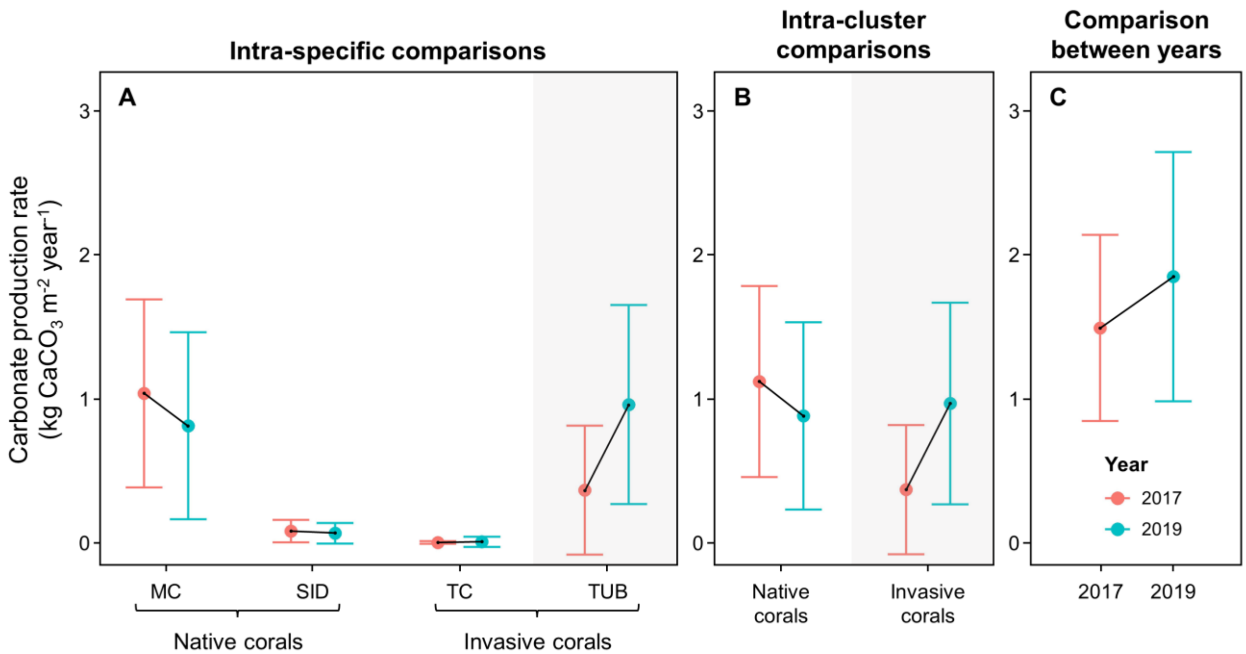

Fig. 6 Inter-annual comparisons between 2017 (orange) and 2019 (light blue) of carbonate production rate (mean kg $CaCO_3$ m^{-2} y^{-1} ± SD) at the top of patches in Cascos Reef, considering **(A)** intra-specific conditions, **(B)** intra-cluster, and **(C)** total production of evaluated species across the years. The light gray shaded area indicates significant differences observed over the years. Abbreviations: MC, *Montastraea cavernosa*; SID, *Siderastrea* sp.; TC, *Tubastraea coccinea*; TUB, *Tubastraea* sp.

4. Discussion

The findings of this study evidence significant differences in coral growth patterns among species inhabiting Cascos Reef (CR). The variability observed in skeletal extension rates, bulk skeletal density, and calcification rates reflects species-specific responses to their patterns, strategies, and growth forms (Hughes 1987; Cairns 1994; Morgan and Kench 2012), influenced by environmental conditions (Lough and Barnes 2000; Manzello 2010; Browne 2012; Mollica et al. 2018) and ecological interactions (Tanner 1997; Lirman 2001; Miranda et al. 2016b).

Invasive corals, particularly *Tubastraea* sp., exhibited higher skeletal extension rates than native species such as *M. cavernosa* and *Siderastrea* sp. These native corals typically exhibit massive and hemispherical forms but may also display encrusting conformations (Leão et al. 2003a). In contrast, the invaders *Tubastraea* sp. and *T. coccinea* have corallites that project vertically relative to the colony base, giving them dendroid and plocoid shapes, respectively (Neves da Rocha et al. 2024). Coral morphology was a significant control on the skeletal extension of coral specimens. More complex forms exhibited faster rates of extension than simpler growth morphologies with continuous growth surfaces (Gladfelter et al. 1978; Hughes 1987; Morgan and Kench 2012). This disparity in growth rates may confer competitive advantages to invasive species, allowing them to rapidly colonize and dominate reef substrates (Vermeij 2005; Creed et al. 2017b).

Information on growth parameters of *Tubastraea* species in the South Atlantic Ocean is scarce, with only one study reporting average linear growth rates of 1.01 and 0.92 cm $year^{-1}$ for *T. coccinea* and *T. tagusensis*, respectively, in rocky reefs of Baía da Ilha Grande (Rio de Janeiro, Brazil), considered high for an azooxanthellate scleractinian coral (De Paula 2007). Compared to the data obtained in the present study, the mean skeletal extension values De Paula (2007) reported were over twice as large. We suggest that the higher productivity of waters along the southeastern coast of Brazil, resulting from cyclical upwelling events (Kjerfve et al. 2021), in comparison to the study area (see Lopes et al. 2009), may influence the skeletal extension rates of the genus *Tubastraea*, given that their primary energy source is plankton available in the water column (Pires-Teixeira et al. 2023).

The native corals *M. cavernosa* and *Siderastrea* sp. assessed in the CR exhibited reduced skeletal extension rates compared to other coral reefs along the east coast of Brazil and worldwide. For instance, Barros and Pires (2006) found *Siderastrea* colonies at a depth of 20 meters growing at approximately 0.25 cm $year^{-1}$ in the Itacolomis reef complex, located on the southern coast of Bahia State, representing more than twice the average skeletal extension rate found in the study area. Similarly, Suggett et al. (2012) identified *Siderastrea* colonies at depths ranging from 3-4 meters growing at approximately 0.20 cm $year^{-1}$ on the upper platforms of chapeirões off Abrolhos reef complex. In reefs with different environmental characteristics (e.g., shallower depths and lower turbidity), *Siderastrea* may demonstrate superior linear growth performance, reaching 0.41 cm $year^{-1}$ in the Gulf of Mexico (DeLong et al. 2014); 0.49 cm $year^{-1}$ in the Florida Straits (Flannery et al. 2017); with records of colonies at 2 meters depth growing up to 0.60 cm $year^{-1}$ in the Rocas Atoll, Brazil (Evangelista et al. 2018). Regarding the species *M. cavernosa*, Suggett et al. (2012) reported a significantly higher skeletal extension rate than that observed for the CR, at 0.62 cm $year^{-1}$ at depths ranging from 3-4 m on the Abrolhos reef complex. Manzello et al. (2015) recorded skeletal extension rates of 0.48 cm $year^{-1}$ at depths of 4-6 m in inshore and offshore locations in the Upper, Middle, and Lower Florida Keys; while Weber and White (1977) documented average skeletal extension rates of 0.32 cm $year^{-1}$ in Belize, the Florida Keys, and Panama, and 0.35 cm $year^{-1}$ in Jamaica. These findings suggest variability in skeletal extension rates among coral populations, likely influenced by local environmental conditions and reef characteristics.

Seawater temperature is a key driver of metabolism and calcification in reef-building corals and, together with other factors (e.g., depth, turbidity, light availability), plays a central role in regulating their growth rates (Lough and Barnes 2000; Lough and Cooper 2011; Kikuchi et al. 2013; Evangelista et al. 2018; Freitas et al. 2019). The higher extension rates recorded for *Siderastrea* sp. in the Gulf of Mexico, Florida Straits, and Rocas Atoll coincide with elevated temperatures in these regions, typically ranging from 27 °C to 30 °C (DeLong et al. 2014; Flannery et al. 2017; Evangelista et al. 2018; Pereira et al. 2024). It is important to note that, although elevated, these temperatures remain within the optimal thermal range for coral calcification and do not indicate thermal stress. In contrast, the Abrolhos Bank and the outer portion of Todos os Santos Bay, where CR is located, exhibit lower average temperatures, between 25 °C and 28 °C (Cirano and Lessa 2007; Kikuchi et al. 2013; Pereira et al. 2024). These regional thermal differences and other environmental and ecological drivers are likely to contribute to the variation in growth rates observed among populations of the same species.

Photosynthesis performed by symbiotic dinoflagellates is the primary energy source for zooxanthellate reef-building corals (Muscatine 1990). Although depth is a crucial factor for the growth performance of these corals (Huston 1985; Watanabe et al. 2019), directly influencing light availability, there seem to be other local forcings in the CR contributing to the lower growth rates exhibited by the assessed native species compared to other reefs in Brazil and worldwide. Miranda et al. (2016) identified significant physical competitive interactions between colonies of native and invasive corals in the RC when there was direct contact, or they were within a maximum distance of 5 cm from each other, with *Siderastrea* sp. showing necrosis in over 50% of the recorded interactions and *M. cavernosa* causing damage to the invader *T. tagusensis*. Despite the different responses to competitive interactions, and even considering that the colonies of native corals assessed in this study did not show signs of mortality, bleaching, or diseases, we suggest that the continuous use of sweeper tentacles (i.e., mesenterial filaments) as a defense mechanism against the elongated polyps of *Tubastraea* spp. (Lapid et al. 2004; Lapid and Chadwick 2006; Santos et al. 2013a; Miranda et al. 2016b) may incur a high energy cost, compromising other crucial functions such as growth or reproduction (Tanner 1997). Sclerochronological studies investigating the linear extension rates of native corals in periods prior to the invasion of *Tubastraea* spp. in the CR may contribute to a deeper understanding of this issue.

The results obtained in this study showed that the average bulk skeletal density varied significantly among coral species, with *T. coccinea* exhibiting lower density than *Tubastraea* sp., *Siderastrea* sp., and *M. cavernosa*. No statistically significant differences in skeletal density were observed between the invader *Tubastraea* sp. and native corals, although statistical tests approached the significance threshold. The growth morphology of invasive coral colonies can directly interfere with the long-term structural integrity and stability of the produced skeletons. The presence of vertically projecting corallites relative to the colony base, along with a density gradient decreasing towards the ends of the polyps, renders the invaders *Tubastraea* sp. and *T. coccinea* more susceptible to physical disturbances and bioerosion processes (Anthony et al., 2008; Edmunds, 2017). Neves da Rocha (2024) demonstrated that *Tubastraea* sp. can add submetric scale complexity to the reef. However, in a scenario where invasive corals dominate the top reef areas of the CR, along with increasingly frequent and intense ocean warming and acidification events due to global climate change (Manzello 2010; Lough and Cooper 2011; Mollica et al. 2018), a greater structural fragility of the reef carbonate framework (Strychar et al. 2021) and changes in biodiversity of this ecosystem (Miranda et al. 2016) are projected.

This study provides the first estimates of bulk skeletal density for the invasive corals *Tubastraea* sp. and *T. coccinea* in the South Atlantic Ocean region. Compared to other reefs worldwide, the density values found were consistent with those observed for species of the same genus exhibiting similar growth patterns. For example, Schuhmacher (1984) reported an average skeletal density of 1.07 g cm^{-3} for *Tubastraea aurea* (plocoid morphotype) in the Pacific region, a value comparable to that obtained for *T. coccinea* in this study. Regarding the native corals assessed, no studies were found providing skeletal density estimates for the South Atlantic Ocean region. However, like other reefs worldwide, *M. cavernosa* and *Siderastrea* sp. also exhibited similar values. Mozqueda-Torres et al. (2018) reported an average density of 1.73 g cm^{-3} for *M. cavernosa* colonies collected at a depth of 4.5 meters in the Puerto Morelos Reef, along the northeastern coast of the Yucatán Peninsula, Mexico. Highsmith et al. (1983) documented an average density of 1.60 g cm^{-3} for colonies of the same species collected at depths between 3 and 7 meters in Belize, which closely matches the density found in our study (1.71 g cm^{-3}). For *Siderastrea* sp., colonies of species within the same genus (*Siderastrea siderea*) collected at depths between 1 and 5 meters exhibited skeletal densities ranging from 1.32 to 1.50 g cm^{-3} in the Puerto Morelos Reef (Carricart-Ganivet et al. 2013) and 1.61 g cm^{-3} in Barbados (Stearn et al. 1977), values similar to those obtained for the same species in our study (1.62 g cm^{-3}). Considering this information and recognizing the consistency and comparability of skeletal density values reported across different studies for invasive and native species, we suggest that this growth parameter (i.e., bulk skeletal density) is minimally influenced by local environmental conditions in the CR, particularly depth.

The coral calcification rate is influenced by skeletal extension and bulk density (Stearn et al. 1977; Edinger et al. 2000). We suggest that the variation in annual calcification rates among the coral species observed in CR is primarily linked to skeletal extension (Morgan and Kench 2012; Kikuchi et al. 2013). Additionally, differences in calcification rates reflect distinct physiological responses to environmental stressors and resource availability (e.g., space, light, and food), highlighting the different growth strategies among species. Our results also demonstrated that invasive corals exhibited calcification efficiency similar to native species, with *Tubastraea* sp. achieving annual calcification rates comparable to *M. cavernosa* and surpassing *Siderastrea* sp. Notably, the mentioned native species are the primary reef builders along the east coast of Brazil (Leão et al. 2003a; Dutra et al. 2006), significantly contributing to reef carbonate production in the region. These findings underscore the complexity of the interaction between growth dynamics, skeletal structure, and carbonate production in coral reef ecosystem construction (Elahi and Edmunds 2007; Holcomb et al. 2014).

The results obtained in the present study also indicate a modification in the structure of the benthic community at the reef top of the Cascos Reef (CR). The invader *Tubastraea* sp. showed a significant increase in its population between 2017 and 2019, despite the native coral *M. cavernosa* still dominating the average coral cover in the study area. On the other hand, crustose coralline algae (CCA), the dominant benthic group in CR, exhibited a significant reduction in their coverage during the evaluated period. Shifts in benthic composition, particularly the increase in *Tubastraea* sp. cover and changes in CCA abundance, suggest dynamic responses to environmental drivers and ecological interactions. Furthermore, changes in carbonate production rates highlight the dynamic nature of reef accretion processes and the contributions of different coral taxa to ecosystem function. While invasive corals contribute significantly to carbonate production, their ecological impacts and interactions with native species must be carefully evaluated to inform conservation and management decisions (Morri et al. 2015; Clements and Hay 2019). Long-term monitoring efforts are essential for assessing the resilience of reef ecosystems and implementing adaptive management strategies to support reef recovery and conservation (Perry et al. 2013; Silverstein et al. 2015).

5. Conclusions

This article presents the first estimates of skeletal growth and carbonate production potential of the invasive sun coral *Tubastraea* on a natural reef in the South Atlantic Ocean. The significant differences observed in coral growth patterns among species highlight the importance of considering species-specific responses to environmental conditions (Lough and Barnes 2000; Manzello 2010; Browne 2012; Mollica et al. 2018) and ecological interactions (Tanner 1997; Lirman 2001; Miranda et al. 2016b). Invasive corals, particularly *Tubastraea* sp., exhibited higher skeletal extension rates and lower bulk skeletal density than native *M. cavernosa* and *Siderastrea* sp., potentially conferring competitive advantages but raising concerns about skeletal long-term stability and structural integrity. Despite the significant contribution of invasive corals to carbonate production and, consequently, to local carbonate reef accretion, the widely documented ecological impacts (Creed et al., 2017; Lages et al., 2011; Santos et al., 2013) and detrimental interactions with native coral species (Miranda et al. 2016b, 2018b) and reef fish (Miranda et al. 2018a; Neves da Rocha et al. 2024) warrant further attention and in-depth studies. Furthermore, the shift in benthic community structure at Cascos Reef, highlighted by a significant increase in invasive coral cover within just two years, presents new challenges to the resilience of South Atlantic coral reefs in the medium and long term. These findings underscore the need to understand the ecological implications of invasive species in reef ecosystems to develop effective management and conservation strategies, particularly considering the inclusion of these ecosystems within or near marine protected areas, such as the Todos os Santos Bay Environmental Protection Area.

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Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) used Grammarly (https://www.grammarly.com/) in order to enhance the fluency and clarity of English writing. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

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Lucas Neves da Rocha: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Funding acquisition. **Ruy Kikuchi:** Conceptualization, Resources, Writing – review & editing, Funding acquisition.

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Data availability

The datasets generated and analyzed during the current study are available from the corresponding author upon reasonable request. The Video Transect Analyzer software (Version 1.0) is available for download at https://bit.ly/VTA1installer.

Declarations

Conflict of interest

The funding source had no involvement in the study design; in the collection, analysis, and interpretation of data; in the writing of the report; and in the decision to submit the article for publication. The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Ethical approval

No ethics approval was required for this study.

CAPÍTULO 3

ARTIGO 2

Submetido e aceito pela: *Marine Biology*

Effects of invasive sun corals on habitat structural complexity mediate reef trophic pathways

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Abstract

Biological invasions have modified habitat structure, forcing changes in ecosystem functions. Structural complexity modulates diversity and trophic pathways, but the roles of invasive species in mediating coral reef habitat attributes and trophic effects are poorly understood. We investigated the influence of invasive corals on reef structural complexity and their implications on reef fish trophic structure. To assess habitat complexity and trophic relationships, we used a digital probe to map reef rugosity and characterized benthic cover and fish abundances by video and visual estimates. We calculated a coral skeleton complexity index (for individual invasive and native colonies) by building high-resolution three-dimensional models with photogrammetry techniques. The study was conducted between February 2018 and March 2019 in Cascos Reef, located on the east coast of Brazil. We reveal that the complex morphology of the invasive coral *Tubastraea* spp. skeleton had a significant positive effect on reef rugosity, contributing to substrate complexity at a sub-metric scale. However, this likely did not promote reef fish diversity but altered the assemblage structure patterns, demonstrated by a negative relationship between coral colony complexity index and abundance of trophic groups such as roving herbivores and omnivores and a positive relationship with planktivores. Thus, our findings support that habitat attribute modification promoted by invasive corals can influence the benthos-fish dynamic, promoting some fish groups to the detriment of others, with pervasive implications for ecosystem functions. Global changes are increasing invasions worldwide, enhancing the need for effective policies for regulation and management to ensure human well-being and ecosystem services.

Keywords: Habitat modification; Biological invasions; *Tubastraea* spp.; Reef fish.

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Introduction

The introduction of invasive species into marine ecosystems has become increasingly frequent (Ruiz et al. 2000; Kolar 2002; Seebens et al. 2013, 2021) and is responsible for generating a series of environmental, social, and economic impacts widely reported around the world (Ruiz et al. 1997; Bax et al. 2003; Molnar et al. 2008). Invasive coral species such as the sun coral (*Tubastraea* spp.) have the successful characteristics of opportunistic organisms, such as rapid growth, competitive efficiency (Wellington and Trench 1985b), ability to colonize different types of substrate and habitats (Creed and Paula 2007) and high fertility rates (Paula et al. 2014b). Furthermore, the absence of zooxanthellae in their tissues and heterotrophic feeding strategy make them independent of light to survive, contrary to other zooxanthellate corals. Native to the Indo-Pacific region (Cairns 1994), this scleractinian coral was introduced into the South Atlantic Ocean in the 1980s (Castro and Pires 2001; Paula and Creed 2004) and expanded its population and geographic limits along the Brazilian coast. *Tubastraea* species are found discontinuously along over 3000 km of the southwestern Brazilian coastline, inhabiting rocky shores, reefs, and artificial substrata (Creed et al. 2017a, c).

Species of the genus *Tubastraea* are usually classified as ahermatypic (non-reef-building) corals (Wells 1993), although there are studies that reinforce their role as reef-builders (Schuhmacher 1984). In this respect, Schuhmacher and Zibrowius (1985) proposed a terminological revision that considers the ability of *Tubastraea* to form an elevated durable carbonate structure and to contribute significantly to the framework of reefs. Recently, Capasso et al. (2022) demonstrated that at the molecular level, *Tubastraea* has specific components in its "calcification toolkit" that give these corals an advantage in calcification strategies. Thus, the colony structure achieved by extra-tentacular budding (Cairns 1994) and the high growth rate of *Tubastraea* spp. suggest that they may play essential roles in the three-dimensional structure of the reef. Quantifying the contribution of each coral species to the topography of the reef substrate makes it possible to assess possible structural changes accurately (Bozec et al. 2015) and implications on the associated fauna.

Structural complexity is a critical attribute in controlling ecological interactions (e.g., intra and inter-specific relationships) and the provision of ecosystem services (e.g., availability of niche areas at different scales) provided by coral reefs (Graham 2014). Reef-building corals create complex physical structures that support high levels of associated biodiversity (Graham and Nash 2013; Rogers et al. 2014). Positive relationships between habitat complexity and fish abundance suggest that reef topography is essential in structuring fish assemblages (Hixon and Beets 1993; McCormick 1994). However, other studies have not found this relationship (Ault and Johnson 1998; Dustan et al. 2013).

Other reef taxa can also contribute significantly to the three-dimensionality of the reef space, such as coralline algae (Leão et al. 2003b; Hamylton et al. 2017), macroalgae (Levin and Hay 1996), soft corals (Wilson et al. 2007; Epstein and Kingsford 2019) and sponges (Diaz and Rützler 2001), as well as the underlying dead matrices formed by the carbonate remains of these organisms later incorporated into the reef, and the geological history of the site itself (Kleypas et al. 2001). On the other hand, physical (e.g., tropical storms) and biological (e.g., coral bleaching and disease) disturbances almost always produce loss and modification of habitat complexity (Wilson et al. 2006; Alvarez-Filip et al. 2011b). Despite the importance of structural complexity for reef ecosystems, the influence of invasive species on them is still understudied.

Despite significant advances in understanding several scientific questions related to sun corals, such as reproduction strategies (Glynn et al. 2008b; Paula et al. 2014b), its dispersion and geographic occupation over time (Sampaio et al. 2012; Carlos-Júnior et al. 2015a; Creed et al. 2017b), ecological interactions with native coral species (Santos et al. 2013a; Miranda et al. 2016b, 2018b) and reef fish (Miranda et al. 2018a), little is known about how this invasive coral, and the increase in its population, is related to the geometric and structural conformation of reefs. Thus, the present study evaluates the influence of the invasive sun coral *Tubastraea* spp. on different scales of structural complexity in a Brazilian reef, examining relationships between individual coral colony complexity and reef substrate rugosity. We also investigated the implication of structural complexity on reef fish trophic groups.

Material and methods

Study area

The study was carried out between February 2018 and March 2019 in Cascos Reef (CR; 13°07′46″S, 38°38′31″W), a complex reef system located in the outer portion of Todos os Santos Bay, east coast of Brazil, Southwest Atlantic (Fig. 7A). Reef morphology in this area is composed of numerous and irregularly spaced patch reefs, which vary in shape and size, surrounded by calcareous and terrigenous sand. The top of patch reefs has reduced dimensions, around 5 to 7 m in diameter. The reef structures extend horizontally up to 100 m long and 13 m high. The depth at the base of the reef reaches 21 m (Miranda et al. 2016b, 2018a).

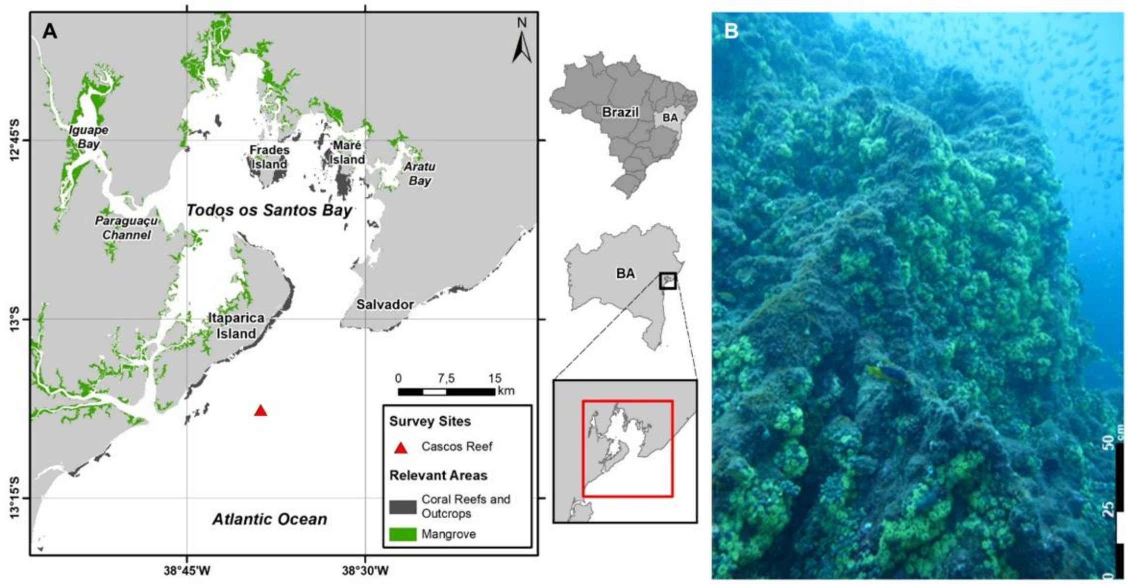

Fig. 7 Study region. **A** Map with the location of Cascos Reef outside the Todos os Santos Bay (Bahia, Brazil). **B** Studied reef with a high cover of the invasive coral *Tubastraea* spp.

The benthic community includes encrusting and branched coralline algae, other macroalgae, sponges, ascidians, bryozoans, octocorals, and scleractinian corals. Native scleractinian coral species are *Montastraea cavernosa*, *Madracis decactis*, *Phyllangia americana*, *Astrangia* spp., *Mussismilia hispida, Siderastrea* sp., and *Meandrina braziliensis*, as well as the calcareous hydroid *Millepora alcicornis*.

Tubastraea tagusensis and *T. coccinea* were first reported in the Southwestern Atlantic in the early 1980s (Castro and Pires 2001; Creed et al. 2017a). The species with plocoid corallites is generally described as *T. coccinea* and a species with dendroid corallites is described as *T. tagusensis*. However, Bastos et al. (2022) found through genetic and morphological studies that there are two morphotypes of the plocoid species, that they still classify as *T. coccinea*, and a third morphotype with dendroid corallites, not representative of *T. tagusensis* despite earlier descriptions describing *T. tagusensis* in Brazil. Thus, this study considered two species of invasive sun coral: *T. coccinea* (plocoid morphotypes) and *Tubastraea* sp. (dendroid morphotype).

Tubastraea spp. have been identified in CR and other regional sites since 2011 (Sampaio et al. 2012). Recent studies by Miranda et al. (2016, 2018a) in CR described baseline patterns of this invasive population initially as clumped colony patches in relatively small areas followed by a population expansion in terms of increasing percent cover along the reef three years after the first assessment was conducted.

Benthic cover

Benthic coverage was estimated using video transects (VT) (adapted from Cruz et al., 2008), recorded in 40 fixed transects of 5 m long by 60 cm wide, randomly positioned on reef tops at least 10 m apart. The transect length was based on CR patch reef morphology, as previously described (i.e., short reef top diameter around 5 to 7 m long), to avoid data acquisition on unconsolidated substrate. The recordings were made with a Canon PowerShot G1 X Mark II camera and a Canon Wp Dc 44 waterproof case, accompanied by a 60 cm long bottom spacer attached to the camera, keeping constant distance and angle to the substrate.

During the survey, the diver maintained a consistent swimming speed of approximately 8 cm s^{-1} above the seafloor. The images were captured in Full HD resolution (1920 x 1080) at an acquisition rate of 29 frames per second. We documented the reef surface between 13 and 19 m (an average of 17 m in depth). The total area of the substrate sampled in VTs was 120 m^2.

The analysis of the VTs was performed using the Video Transect Analyzer software (Version 1.0), developed by the Research Group on Coral Reefs and Global Change (RECOR) at the Federal University of Bahia (available for download at https://bit.ly/VTA1installer). The percent cover of benthic organisms was estimated by identifying them at randomly cast points in a set of non-overlapping images generated consecutively, covering the entire surface of the substrate recorded in each VT. Furthermore, we counted and classified into size classes (five intervals: < 5 cm, 5 – 10 cm, 10 – 30 cm, 30 – 50 cm, > 50 cm) the colonies of native corals (*Siderastrea* sp. and *M. cavernosa*) and invasive corals (*T. coccinea* and *Tubastraea* sp.) in each of the 40 transects. *Siderastrea* sp. and *M. cavernosa* were chosen for this analysis because they are among the main reef builders of Brazilian reefs (Leão et al. 2003b; Dutra et al. 2006). Markings of known dimensions on the transects were used as a scale reference during analysis of the VTs. The selection of size classes considered the frequency of observed coral colony sizes in the VTs.

Structural complexity

Colony complexity

We developed three-dimensional models of invasive (*Tubastraea* sp. and *T. coccinea*) and native (*M. cavernosa* and *Siderastrea* sp.) coral skeletons using digital photogrammetry (Fig. 8A, B) to estimate coral colony complexity. Colony samples included adult *Tubastraea* spp. colonies of at least 5 cm in diameter. The native species were selected based on their abundance and massive hemispherical shape, with dimensions around 10 cm in the central growth axis. Specimens of each species (*n* = 3 for both *Tubastraea* species, *n* = 2 for both native species) were collected at 16 and 19 m depth. All colonies were healthy without signs of mortality, bleaching, or diseases.

The coral colonies were photographed sequentially at different angles to cover their entire area in detail (adapted from Veal et al., 2010; Ferrari et al., 2017). For this, we used a turntable, a tripod, a camera (Canon EOS 5D Mark III) attached to a notebook (Dell Inspiron 15 5566 - Intel ® Core ™ i3-4005U CPU 1.70GHz, RAM 4GB, HD 500GB, Windows 10 ID 00327-30358-60052-AAOEM), a lighting system consisting of two softboxes and a photographic software for remote control and shooting (Canon EOS Utility). The photographs (JPEG; 5760 x 3840 pixels) were imported in packages (100 photos for each copy) into Autodesk PhotoRecap software (Education License, SN 901-19313022) for subsequent three-dimensional reconstruction. In this process, a Desktop computer

Dell Precision Tower 3620 - Processor Intel ® Xeon ® CPU E3-1270 v6 @ 3.80GHz, RAM 32GB, HD GB, Windows 10 ID 00330-50656-21558-AAOEM.

After three-dimensional reconstruction, digital models of specimens were analyzed using Meshlab v1.3.3 software (Cignoni et al. 2008). Geometric variables such as length, height, width, and surface area were estimated using the software's measurement tools. Then, it was possible to generate a mesh determined by the most external points of the digital model (Convex Hull) and to calculate the surface area of the polygon resulting from the connection of such points (Agudo-Adriani et al., 2016).

The individual colony complexity (CC) was estimated considering the ratio between the actual surface area and the convex contour surface area generated by connecting the most external points of the respective digital model. Finally, each species complexity index (CC_{sp}) was determined from the average of the individual complexities of the collected colonies, according to Equation (1) below:

$$CC_{sp} = \frac{CC_1 + CC_2 + \cdots + CC_n}{n} \tag{1}$$

where CC_n is the individual complexity of each of the colonies collected, and n is the absolute number of colonies of a given species of coral.

By measuring and quantifying the different geometric growth patterns, it is possible to use discrete values (Denis et al. 2017) calculated specifically for each species in associated analyses and index constructions.

With the number of colonies per size class (obtained in the analysis of benthic coverage by the VTs) and the species complexity index (CC_{sp}), it was possible to estimate the individual contribution index of each species to the structural complexity of the transects (CCI_{sp}) evaluated in CR, parameterized according to Equation (2) below:

$$CCI_{sp} = \sum_{i=A}^{E} N_{Class_i} \times W_{Class_i} \times CC_{sp} \tag{2}$$

where N_{Class_i} is the number of colonies per size classes ($Class_A$ < 5 cm; $Class_B$ 5 – 10 cm; $Class_C$ 10 – 30 cm; $Class_D$ 30 – 50 cm; $Class_E$ > 50 cm); W_{Class_i} is the weight assigned to each size class ($Class_A$ = 1; $Class_B$ = 2; $Class_C$ = 3; $Class_D$ = 4; $Class_E$ = 5); and CC_{sp} is the species complexity index.

The individual contribution of invasive corals to the complexity of each transect ($CCI_{Invader}$) was calculated as the sum of the indices obtained for *Tubastraea* sp. and *T. coccinea*. For native corals, the same attribute was calculated by adding the index obtained for *M. cavernosa* and *Siderastrea* sp. (CCI_{Native}).

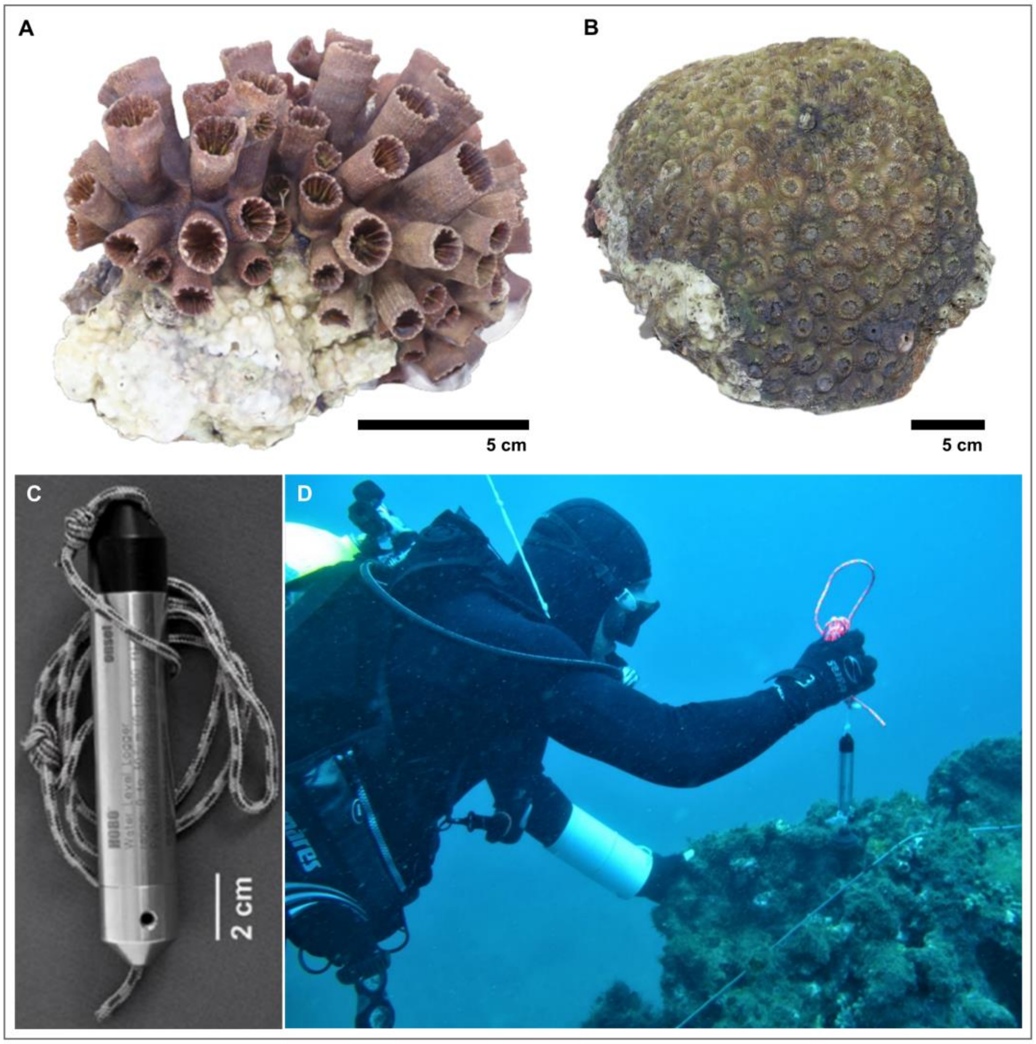

Fig. 8 Assessment of reef structural complexity at coral colony and reef scales: digital skeleton models developed by photogrammetry of the (**A**) dendroid invasive coral *Tubastraea* sp. morphotype and (**B**) hemispheric massive native coral *M. cavernosa*; (**C**) the high-resolution depth probe used to measure reef scale rugosity and (**D**) diver taking measurements with the probe at the reef top in the study site.

Reef scale rugosity

Reef rugosity was estimated over the same 40 fixed transects randomly positioned on reef tops using a digital probe (Onset Computer Company #U20_001-02, Fig. 8C) as described by Dustan et al. (2013). The measurements were taken by a diver carrying a probe swimming along the transect as close as possible to the contour of the substrate, avoiding any direct contact with the bottom (Fig. 8D). The probe was kept at a maximum distance of 1 cm from the substrate during all measurements. The estimates are parameterized using water column pressure every second along the transect. A 500g pointed plummet was added to the gauge's lower end to maintain probe stability, reducing the pendulum effect generated by the current and the diver's displacement. Additionally, a second probe (same model, operational settings, and time reference) was used in a static position relative to the reef and to the diver's movement to measure the height of the waves during the acquisition of digital rugosity data and to remove wave variability in post-processing. The typical error of the digital probes used, which reflects the accuracy of these instruments, is ±0.05% (1.5 cm water column).

The data obtained with the probe were downloaded through an optical base and communication software from the same manufacturer. They were corrected based on the atmospheric pressure measured at the surface, converted into depth units (m), exported to an electronic spreadsheet, and treated according to the metadata records (start and end time of each transect). Each record made by the probe (second by second) carried by the diver was corrected based on the temporally correlated wave height data recorded by the stationary probe, either by adding or subtracting this height depending on the wave phase (crest or trough) relative to its zero amplitude point. The substrate contour along each transect was calculated by subtracting the deepest point from all other depths (relative depth).

Considering that the standard deviation describes the variation of a set of measurements, we chose to characterize the structural complexity as the standard deviation of the sensor output data (Digital Reef Rugosity or DRR_{STD}), as applied by Dustan et al. (2013). This way, a DRR_{STD} value was obtained for each transect. Reef rugosity (e.g., amplitude variations in the height of a surface) is a traditional proxy indicator for structural complexity (Denis et al. 2017).

Fish trophic structure

The fish assemblages were characterized through underwater visual censuses along the established transects 5 m in length, but 2 m in width. In the belt transect method, the diver swims the 5 × 2 m transect path twice, first looking at the fish in the water column and then returning to record small and cryptic species in the substrate. The diver remained static for one minute before starting each of the visual censuses to avoid scaring away highly mobile species such as terminal roving herbivores (Nunes et al. 2016; Wetz et al. 2020). Fish richness and abundance were recorded and then standardized as the number of individuals per square meter ($N\ m^{-2}$). Fish species were identified and classified into seven trophic groups based on literature: territorial herbivore (TH), planktivore (PL), roving herbivore (RH), omnivore (OM), carnivore (CA), mobile invertivore (MI), and sessile invertivore (SI) (Floeter et al. 2004; Ferreira et al. 2004; Halpern and Floeter 2008; Longo et al. 2014).

Statistical analysis

We used Principal Component Analysis (PCA) to characterize possible relationships between the benthic groups observed at the top of patches in Cascos Reef (CR) based on a Covariance Matrix (raw data standardized as a percentage of substrate cover).

Linear models (single and multiple regressions) were used to evaluate the associations between DRR $_{STD}$, percentage coverage of native and invasive corals, and the indices of specific contribution to CR's structural complexity (CCI). The Shapiro-Wilk and Fligner-Killeen tests were used to test the normality and homogeneity of residual variance, respectively. Data were transformed (square root + 0.5) when necessary to fulfill the homogeneity assumption. The significance level (α) adopted in the analysis was 0.05.

Generalized Linear Models (GLMs) were used to evaluate the combined effect of structural complexity and benthic cover on the species richness and abundance of fish trophic groups in the CR. The correlation between all environmental predictors was assessed using the Spearman test to avoid collinearity (r values > 0.70) within the same model (see Supplementary Information, Table SI 1). To avoid the phenomenon of overdispersion, when necessary, we adjusted the models initially conceived from a Poisson distribution (commonly used for abundance and species richness data) to a negative binomial, considering as a parameter for evaluating the ratio between the residual error and the degrees of freedom (values should approach the maximum of 1 to indicate a good model fit). Null models were also designed to test the environmental predictors' lack of effect.

Finally, all models designed for the species richness and abundance of each fish trophic group were submitted to a model selection approach based on the Akaike information criterion corrected for small samples (AICc), where lower values of AIC indicate better model fits. Models with AICc differences (ΔAICc) of less than two were considered equiprobable. The Akaike weight, which expresses the normalized relative probability of each model, was also used as a selection criterion (Burnham and Anderson 2004; Anderson 2008). Models that met these criteria were assumed to be equally plausible in explaining the observed patterns.

All analyses were performed using R 4.2.1 software (R Development Core Team, www.r-project.org): the packages ‘FactoMineR’ and ‘factoextra’ were used for PCA analyses; the package ‘bbmle’ was used for the GLMs and model selection.

Results

Benthic structure patterns

The top three most abundant benthic groups were turf algae (TURF, mean percent coverage ± standard deviation: 32.2 ± 9.2%, n = 40), crustose coralline algae (CCA, 23.7 ± 6.5%), and corals (22.3 ± 10.1%; native and invasive species). Calcareous articulated algae (CAA) covered 19.3 ± 8.0%, followed by macroalgae (1.4 ± 2.5%), sponges (1.0 ± 1.5%), and echinoderms (less than 0.1 ± 0.1%) (see Supplementary Information, Table SI 2.1 and Fig. SI 2.1). PCA analysis showed negative covariance between the invasive coral *Tubastraea* sp. cover and TURF and between CCA and CAA (see Supplementary Information, Fig. SI 2.2).

Coral cover in the CR varied from 3% to 41%. Among the native hermatypic species (15.3 ± 8.2%, n = 40), *M. cavernosa* was the most abundant (11.8 ± 7.4%), followed by *Siderastrea* sp. (1.5 ± 1.3%), *M. decactis* (1.1 ± 2.3%) and *M. hispida* (0.9 ± 1.5%). Among the invasive ahermatypic corals (6.9 ± 8.6%), *Tubastraea* sp. (6.8 ± 8.4%) predominated compared to *T.* coccinea (0.1 ± 0.7%) (see Supplementary Information, Table SI 2.2).

Colony complexity and contribution to reef rugosity

The photogrammetry of coral colonies showed different levels of geometric complexity of the species evaluated. The three-dimensional models of colonies varied significantly in size (height, length, and maximum width) and area (colony surface area and convex surface area formed by the colony endpoints). Invasive species exhibited higher complexity index values CC_{sp} (*Tubastraea* sp.*:* 0.77 ± 0.08; *T. coccinea:* 0.74 ± 0.11) compared to native species (*M. cavernosa:* 0.18 ± 0.01; *Siderastrea* sp.: 0.11 ± 0.02) (see Supplementary Information, Table SI 3).

A positive association was observed between coral cover (invaders and natives) and the respective indices of contribution to complexity (Table 7). Furthermore, the contribution of invasive corals to complexity ($CCI_{Invader}$) was positively associated with reef rugosity (DRR_{STD}), while native corals (CCI_{Native}) did not exhibit a significant association (Multiple linear regression: $r2 = 0.16$, $F = 3.54$; $CCI_{Invader}$, $P < 0.05$; CCI_{Native}, $P > 0.05$) (Table 7; Fig. 9; see Supplementary Information, Table SI 4).

Table 7 Statistical output parameters of regression analyses (single and multiple) performed between Digital Reef Rugosity (DRR_{STD}) at reef scale, coral cover (percentage), and the complexity contribution index (CCI). Highlight in bold for significant analyses (i.e., P values < 0.05).

	Coefficient	**T**	**P**	**Standard error**	**r2**	**df**	**F**
DRR_{STD} x Coral cover				0.10	0.11	37	2.32
Intercept	0.87	13.46	**< 0.001**	0.06			
Invasive coral	0.02	2.15	**0.038**	0.01	0.10		
Native coral	0.01	0.63	0.530	0.01	0.00		
DRR_{STD} x CCI				0.09	0.16	37	3.54
Intercept	0.85	10.74	**< 0.001**	0.80			
$CCI_{Invader}$	0.01	2.65	**0.012**	0.00	0.15		
CCI_{Native}	0.02	0.72	0.476	0.02	0.00		
% Coral Invader x $CCI_{Invader}$				0.36	0.95	38	709.5
Intercept	0.29	3.13	**0.003**	0.09			
$CCI_{Invader}$	0.25	26.64	**< 0.001**	0.09			
% Native Coral x CCI_{Native}				0.68	0.64	38	67.92
Intercept	-0.10	-0.20	0.842	0.49			
CCI_{Native}	1.41	8.24	**< 0.001**	0.17			

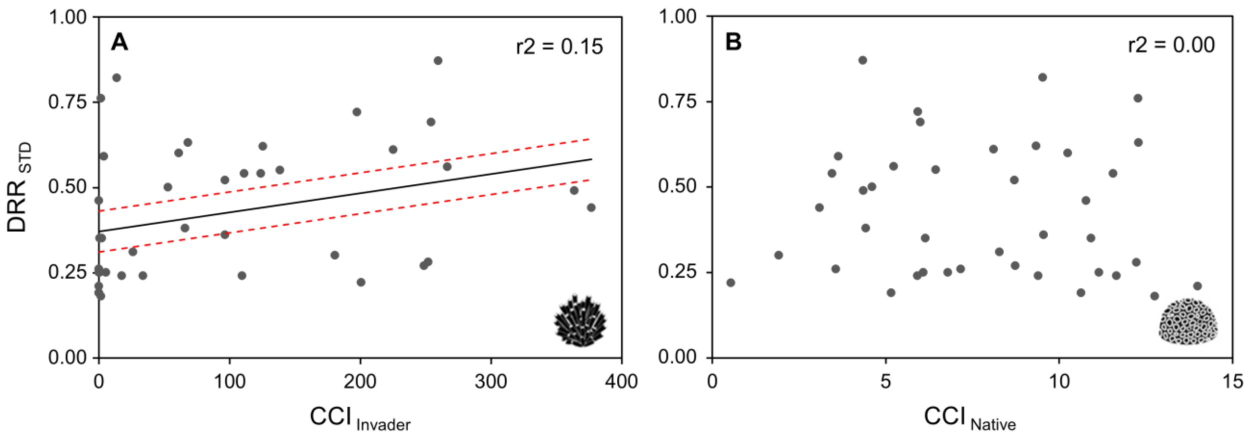

Fig. 9 Relationship between Digital Reef Rugosity (DRR $_{STD}$) and the Individual Contribution Index to Reef Complexity (CCI) for (**A**) invasive *Tubastraea* spp. and (**B**) native coral species. Black dots indicate the 40 transects evaluated. A solid black line represents the significant linear model for the invasive species. Red dashed lines indicate the confidence interval (95%).

Digital reef rugosity

The average sampling rate of digital rugosity on the studied reef was 13.4 ± 3.0 samples m^{-1} (n = 40) and ranged between 9.2 and 22.6 samples m^{-1}. There was no relationship between sampling rates and the digital rugosity (DRR $_{STD}$). The stationary probe recorded wave heights up to 0.6 m during data acquisition.

The DRR $_{STD}$ values varied significantly between the different patch reefs, evidencing a complex morphology of the substrate (see Supplementary Information, Table SI 4). DRR $_{STD}$ and invasive coral cover were positively associated (Multiple linear regression: $r2 = 0.11$, $F = 2.32$, $P < 0.05$). However, no significant differences were found between DRR $_{STD}$ values and native coral cover (Table 7).

Fish assemblages and relationship with benthic descriptors

A total of 6,049 individuals, 52 species, 21 fish families, and seven trophic groups were observed on the reefs (see Supplementary Information, Table SI 5). Mobile invertivore (MI) was the dominant trophic group, accounting for 49% of all fish observed, followed by planktivore (PL, 43.6%), roving herbivore (RH, 2.6%), carnivore (CA, 1.6%), territorial herbivore (TH, 1.5%), omnivore (OM, 0.9%), and sessile invertivore (SI, 0.8%). The most abundant species for each trophic group were *Haemulon aurolineatum* (MI), *Chromis multilineata* (PL), *Sparisoma axillare* (RH), *Cephalopholis fulva* (CA), *Stegastes fuscus* (TH), *Abudefduf saxatilis* (OM) and *Holacanthus tricolor* (SI).

No predictor variable could explain the variability in fish species richness along the study area, as indicated by a significant null model (see Supplementary Information, Table SI 6.1). Seven models were considered equally plausible to explain the relationship between the abundance of TH fish and structural complexity and benthic cover in the Cascos Reef (CR). However, only the model containing the macroalgae (MAC) predictor was significant (negative relationship). For RH, four models were considered equally plausible to explain this relationship, but only the model containing both calcareous articulated algae (CAA) and CCI $_{Invader}$ was significant (negative relationship; Fig. 10). For PL, 15 models proved to be equiprobable, and only two of them were significant, the first containing the predictors CAA and CCI $_{Invader}$ together (positive relationship; Fig. 10) and the second model containing crustose coralline algae and turf algae (TURF) (negative relationship). There were five equiprobable models for OM fish, and only one, containing the predictor CCI $_{Invader}$, was significant (negative relationship; Fig. 10). For SI, two models were considered equiprobable, and only the one containing the TURF predictor was significant (positive relationship). On the other hand, CA and MI fish showed significant null models (Table 8). Specifically, on the environmental descriptor used to represent the structural complexity at reef scale (DRR $_{STD}$), no significant model could relate it to the abundance of any trophic groups (see Supplementary Information, Table SI 6.2).

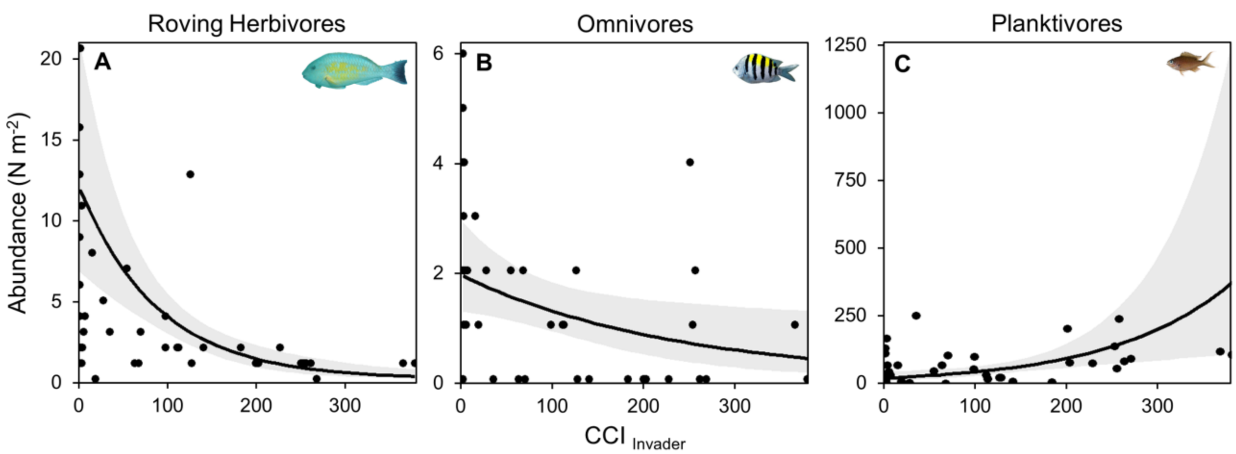

Fig. 10 Relationship between fish trophic group abundance (N m^{-2}) and complexity contribution index of invasive corals (CCI $_{Invader}$). Fish illustrations represent the most abundant species within the respective trophic groups evaluated: (**A**) Roving Herbivores: *Sparisoma axillare*; (**B**) Omnivores: *Abudefduf saxatilis*; (**C**) Planktivores: *Chromis multilineata*. Black dots indicate the replicate transects (n = 40). The black line represents the significant GLM, and light gray represents the confidence interval (95%).

Table 8 Generalized Linear Models of relationships between environmental predictors (benthic cover and complexity indices) and abundance of reef fish trophic groups. Only models with significant predictor variables or null models are shown (i.e., P values < 0.05). CAA, Calcareous articulated algae; CCA, Crustose coralline algae; TURF, Turf algae; MAC, Macroalgae; and CCI $_{Invader}$, Contribution index of invasive corals to reef complexity.

Trophic Group	**Model**	**Estimated**	**Standard error**	**Z**	**P**
Territorial Herbivores (TH)	**MAC**				
	Intercept	0.967	0.118	8.167	**< 0.001**
	MAC	-0.161	0.068	-2.354	**0.019**

Trophic Group	Model	Estimated	Standard error	Z	P
Roving Herbivores (RH)	**CAA + CCI $_{\text{Invader}}$**				
	Intercept	2,774	0.370	7.504	**< 0.001**
	CAA	-0.050	0.017	-2.944	**0.003**
	CCI $_{\text{Invader}}$	-0.007	0.002	-4.647	**< 0.001**
Planktivores (PL)	**CAA + CCI $_{\text{Invader}}$**				
	Intercept	2,712	0.470	5.774	**< 0.001**
	CAA	0.054	0.020	2.658	**0.008**
	CCI $_{\text{Invader}}$	0.003	0.001	2.126	**0.033**
	CCA + TURF				
	Intercept	6,735	0.885	7.609	**< 0.001**
	CCA	-0.065	0.025	-2.546	**0.011**
	TURF	-0.035	0.018	-1.986	**0.047**
Omnivores (OM)	**CCI $_{\text{Invader}}$**				
	Intercept	0.643	0.209	3.075	**0.002**
	CCI $_{\text{Invader}}$	-0.004	0.002	-2.303	**0.021**
Carnivores (CA)	**Null**				
	Intercept	0.876	0.105	8.354	**< 0.001**
Sessile Invertivores (SI)	**TURF**				
	Intercept	-2.499	0.900	-2.776	**0.006**
	TURF	0.077	0.025	3.093	**0.002**
Mobile Invertivores (MI)	**Null**				
	Intercept	4.305	0.137	31.540	**< 0.001**

Discussion

Influence of invasive corals on structural complexity

The colony complexity of the invasive species' dendroid (*Tubastraea* sp.) and plocoid (*T. coccinea*) morphotypes was higher than two common native corals with massive and hemispherical shapes and positively related to the general rugosity of the reef. While there may be a positive contribution of the complexity provided by *Tubastraea* spp. (CCI $_{\text{Invader}}$) for general reef rugosity (DRR $_{\text{STD}}$), the relationship found was weak. The interrelationship between the intrinsic characteristics of the main reef builders (Kleypas et al. 2001; Denis et al. 2017; Urbina-Barreto et al. 2021), the processes acting on the site (Wilson et al. 2006; Alvarez-Filip et al. 2011b), and the different spatial scales of evaluation (McCormick 1994a; Knudby and LeDrew 2007), define a reef's structural complexity. The high complexity colony morphology and linear growth rate of *Tubastraea* spp. (Paula et al. 2014b) compared to native species and its ability to colonize different types and conformations of substrates (Mizrahi et al. 2014; Miranda et al. 2018b) are characteristics that can influence the three-dimensionality of the reef space. As such, we suggest that this invasive organism may be starting a process of modifying the natural sub-metric geometry of Cascos Reef (CR). Nevertheless, further studies should be conducted to delve deeper into this issue.

The results obtained in the present study provide evidence that sun coral colonies can add complexity to the CR substrate on a sub-metric scale. Under specific conditions, *Tubastraea* spp. can behave as a reef-building coral and incorporate calcium carbonate into the reef's structural framework, contributing to its three-dimensionality (Schuhmacher and Zibrowius 1985; Capasso et al. 2022b). The habitat's structural complexity is one of the determining factors in local abundance and diversity, significantly influencing competition and predation events (Hixon and Beets 1993; Almany 2004). However, in the case of CR, such added complexity is due to the increase of this invader, whose negative impacts on native corals are documented in the literature (Creed 2006; Santos et al. 2013a). More specifically, in the CR itself, Miranda et al. (2016) evaluated competitive interactions and described the impacts of sun coral on the native coral assemblage, showing that *Tubastraea* sp. (dendroid) caused high tissue necrosis of *Siderastrea stellata, M. hispida,* and *M. decactis* but did not affect *M. cavernosa*, the species dominant at the top of this patch reef system.

It remains important to characterize the complexity of other frequently occurring coral species on the Brazilian coast, such as *M. decactis* (nodular form), *Mussismilia hispida*, *Mussismilia braziliensis,* and the hydrocoral *Millepora* spp. (branching form). The latter, in particular, comprises the only branching coral species found in Brazil, playing an essential role in maintaining the complexity of Brazilian reefs. Although not found in study site sampling, *Millepora* spp. is quite common on shallow reef edges and coral communities of Brazil (Castro and Pires 2001). The structural complexity generated by the branching forms of these species provides habitat for various fish and invertebrates, thereby increasing reef biodiversity (Alvarez-Filip et al. 2009, 2011a; Graham and Nash 2013b).

No relationship was found between individual native corals' complexity (CCI_{Native}) and general rugosity of the reef (DRR_{STD}). Several studies associate scleractinian corals with the structural complexity of reefs, where massive corals appear as the primary provider of three-dimensionality and modulator of the substrate (Guest et al. 2012; Graham and Nash 2013b; Rogers et al. 2014). The results suggest that the geometries of the native colonies, typically massive hemispherical but sometimes also encrusting, combined with the continuous growth of these species over thousands of years, are "confused" with the characteristic contour of the CR, shaped over time by historical geomorphological factors, and thus are not distinguished by this method of obtaining the DRR_{STD}. Previous studies also found no correlation between coral cover and complexity in reefs worldwide where coral cover is low (Graham et al. 2009), which seems to be the case for CR and Brazilian coral reefs in general. Despite the possibility of scleractinian corals (both native and invasive) contributing to the supply of carbonate structures, it seems that geomorphological factors (both endogenous and exogenous) still play significant roles in the overall structural complexity observed in CR.

Influence of structural complexity on the trophic structure of fish

The complexity provided by sun coral colonies did not promote reef fish diversity but likely boosted changes in the reef fish assemblage structure. The models showed the $CCI_{Invader}$ does not influence fish richness but is an active modulator of trophic structure, associating negatively with roving herbivores (RH) and omnivores (OM) and positively with planktivores (PL).

The results obtained in the present study point to the existence of a negative relationship between the complexity provided by invasive corals ($CCI_{Invader}$) and the abundance of RH. Furthermore, the negative correlation observed between the coverage of *Tubastraea* sp. (dendroid) and turf algae (TURF) indicates a reduction in the direct availability of food resources for RH in a scenario of increased sun coral cover. RH fish feed mainly on detritus and algae but are also commonly observed feeding on the delicate tissues of scleractinian corals (Ferreira et al. 2004; Halpern and Floeter 2008; Francini-Filho et al. 2010). Miranda et al. (2018a), when evaluating the feeding rates of this group on the same reef, found an exponential decrease in substrate bites when the sun coral cover increased. Three main factors can be potential causes of the negative relationship observed: the low palatability of *Tubastraea* spp., due to the production of chemical defenses and allelochemicals (Lages et al. 2010, 2012; Moreira and Creed 2012); the physical difficulty in accessing the surfaces for herbivory imposed by the dendroid and plocoid shapes of the corallites of these species (Miranda et al. 2018a); and the reduction in the direct availability of food resources for herbivory, in this case, TURF, caused by the occupation of space by *Tubastraea* sp. (dendroid). The combined effect of these factors is potentially critical for RH. This fish group is essential for maintaining reef health, acting directly on algal productivity and coral recruitment (Bonaldo and Bellwood 2011). Structurally, these animals also reshape the landscape built by scleractinian corals by scraping the hard carbonate surfaces and transporting sediment around the reef (Bellwood 1996; Goatley and Bellwood 2012).

We did not find a positive association between the complexity provided by invasive corals ($CCI_{Invader}$) and the abundance of territorial herbivores (TH). Such an association was expected when considering the close relationship of the species of this group with the substrate, the relatively small average size of individuals, and the good capacity for food choice (Ferreira et al. 2004), which allows them to graze and shelter between colonies of sun coral and actively maintain their territories (Miranda et al. 2018a). The same authors report that the reduction in food visibility (detritus and algae on herbivory surfaces) due to the three-dimensionality provided by invasive corals may increase competition between TH and RH, possibly pushing the latter group away to areas where *Tubastraea* spp. are less abundant and thus triggering changes in commonly observed benthos-fish interactions.

The abundance of PL fish was positively associated with $CCI_{Invader}$ and calcareous articulated algae (CAA), and negatively associated with crustose coralline algae (CCA) and TURF. The fish in this trophic group feed mainly on macro- and microzooplankton (Ferreira et al. 2004). Fish with diurnal habits are known to invest in individual prey (mainly copepods, larvae, and fish eggs) based on visual cues (Thresher 1983), and predominantly nocturnal fish tend to roost in caves and crevices during the day, leaving their hiding places shortly after sunset for hunting and breeding activities (Koeda et al. 2013). Such observations suggest that the three-dimensionality provided by sun coral colonies, in conjunction with the availability of hiding places shaped by CAA, may favor this trophic group against interspecific predators and competitors (e.g., RH and OM), making areas with such characteristics attractive to PL. In addition, more complex and prominent surfaces can act as traps for plankton available in the water column, facilitating the food supply to this trophic group. On the other hand, more exposed areas of the reef, where the presence of CCA and TURF are dominant, may represent an environment with a greater risk of predation.

We also observed a negative relationship between the complexity provided by invasive corals ($CCI_{Invader}$) and the abundance of OM. These fish are adapted to different reef environments and have a relatively flexible diet, including animals and algae. Factors such as seasonality and environmental disturbances trigger and modulate their eating habits (Ferreira et al. 2004). In this regard, we suggest that, as observed for RH, the same three main factors directly influence this relationship. Considering the flexibility to access different nutritional sources, OM reef fish tend to avoid parts of the reef with the complexity provided by the invasive coral *Tubastraea* spp. and with less availability of TURF. The abundance of MI, SI, and CA fishes were not related to the complexity provided by invasive corals ($CCI_{Invader}$).

As for the complexity provided by native builder corals (CCI_{Native}), we did not find a relationship with any trophic group of fish. Almany (2004) suggests that complexity plays an essential role in structuring reef fish assemblages, but the main mechanisms of this relationship have not been well characterized. In this regard, we raise two possibilities: the first one is that in the Cascos Reef, the hemispherical, massive, and often encrusting pattern of native corals, combined with the continuous growth of these species over thousands of years, has led to the development of similar relief features throughout the entire reef. This pattern may exert a homogeneous influence on prey-predator relationships operating in that area. The second is that other benthic organisms (e.g., CCA, TURF, macroalgae, and invasive corals) can also influence the effect of structural complexity on the occurrence of reef fish. The simultaneous occurrence of both possibilities described above appears to be a plausible hypothesis but requires further investigation.

Conclusions

This study demonstrated that sun coral invasion may have affected the reef structure complexity at a sub-metric scale and indirectly reef fish trophic structure. The three-dimensional format of invasive coral skeletons, rapid growth, and substrate occupation may have contributed to this aspect. Changes in benthic species composition and reef geometry can modify the availability of food resources consumed by fish groups, such as roving herbivores (RH), reducing their activities and benefiting other fish groups, like planktivores. Although RH abundance was relatively low in the study area, their foraging activity plays key ecosystem functional roles (e.g., algal control, bioerosion, and sediment transport), significantly contributing to coral reef energy flow (Bonaldo et al. 2014). This kind of effect demonstrates how dependent and interconnected habitat structure and benthos-fish relationships are. It corroborates previous evidence of the pervasive impacts of this invasive coral on the ecosystem functions of coral reefs.

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Statements and Declarations

Author contributions

LSNR, JACCN, RJM, and RKPK designed the study; LSNR performed fieldwork; RKPK and LSNR provided infrastructure/material/technical support; LSNR, JACCN, and RJM analyzed the data; and LSNR, JACCN, RJM, and RKPK contributed to the manuscript.

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Data availability

The datasets generated and analyzed during the current study are available from the corresponding author upon reasonable request. The Video Transect Analyzer software (Version 1.0) is available for download at https://bit.ly/VTA1installer.

Conflict of interest

The funding source had no involvement in the study design; in the collection, analysis, and interpretation of data; in the writing of the report; and in the decision to submit the article for publication. The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Ethical approval

No ethics approval was required for this study.

CAPÍTULO 4
CONCLUSÕES

A invasão do coral-sol *Tubastraea* no Oceano Atlântico Sul tem provocado alterações significativas na complexidade estrutural dos recifes e modificado a estrutura trófica dos ecossistemas recifais. A presença dessa espécie de coral invasora, caracterizada por taxas elevadas de extensão linear e densidade esquelética próxima à dos corais nativos *M. cavernosa* e *Siderastrea* sp., tem implicações para a estabilidade e integridade estrutural de longo prazo dos recifes invadidos, visto que as extremidades do seu esqueleto tendem a ser menos densas do que as bases, tornando-os mais susceptíveis às mudanças climáticas globais. Embora o invasor *Tubastraea* contribua significativamente para a produção de carbonato, com taxas de calcificação semelhantes aos corais construtores nativos, seu crescimento rápido e ocupação de substratos têm modificado a composição da comunidade bentônica e a geometria dos recifes, impactando a disponibilidade de recursos alimentares para os peixes recifais. Essas mudanças na composição bentônica têm efeitos indiretos na estrutura trófica dos peixes, afetando principalmente as atividades dos herbívoros móveis (RH) e favorecendo outros grupos de peixes, como os planctívoros. A redução na abundância de RH, considerando seu importante papel ecossistêmico no controle de algas e transporte de sedimentos, destaca a interconectividade entre a estrutura do habitat e as relações entre bentos e peixes.

No geral, os achados desse trabalho enfatizam a necessidade de compreender com mais profundidade os impactos ecológicos de espécies invasoras nos recifes de coral. Diante da crescente ameaça das bioinvasões, estratégias eficazes de gestão e conservação devem abordar as interações entre espécies invasoras e nativas, a complexidade estrutural dos recifes e sua estrutura trófica. Por fim, vale ressaltar que o trabalho apresentou as primeiras estimativas de crescimento esquelético e potencial de produção de carbonato do coral-sol *Tubastraea* em um recife natural no Oceano Atlântico Sul, representando um passo relevante para compreender detalhadamente os padrões de crescimento desse organismo invasor e as possíveis implicações associadas à sua dispersão ao longo da costa do Brasil.

APÊNDICE A – JUSTIFICATIVA DA PARTICIPAÇÃO DOS CO-AUTORES NO ARTIGO 2

Ruy Kenji Papa de Kikuchi: Lattes – http://lattes.cnpq.br/8391627429679768

Orientador da tese, é professor Titular do Departamento de Oceanografia da Universidade Federal da Bahia. Leciona desde 2002, na graduação dos cursos de Geologia e Oceanografia, na pós-graduação em Geologia e em Ecologia. É pesquisador de produtividade científica do CNPq desde 2002, atualmente bolsista nível PQ-1C. Graduado em Geologia pela Universidade de São Paulo (1986), tem Mestrado em Geologia pela Universidade Federal da Bahia (1994) e Doutorado em Geologia pela Universidade Federal da Bahia (2000). É revisor ad hoc dos periódicos Biota Neotropica, Anais da Academia Brasileira de Ciências (0001-3765), *Geochimica et Cosmochimica Acta*, *Limnology and Oceanography*, entre outros. Tem experiência na área de Oceanografia, com ênfase em Oceanografia Geológica, atuando principalmente nos seguintes temas: recifes, corais, Abrolhos, Atol das Rocas, conservação de ecossistemas e mudanças climáticas globais. Integra o INCT Ambientes Marinhos Tropicais onde coordena os GTs "Recifes e Ecossistemas Coralinos" e "Derrames de óleo (grupo executivo do Projeto Emergencial para resposta a questões do acidente com óleo, em consórcio com os INCT MAR-COI e INCT PRO-OCEANO)". Integra também a sub-rede Zonas Costeiras da Rede Clima, é membro do Grupo de Assessoramento Técnico do Plano de Ação Nacional para a conservação dos ambientes coralinos, e conselheiro do Conselho Gestor da APA Tinharé-Boipeba (BA).

Ricardo Jessouroun de Miranda: Lattes – http://lattes.cnpq.br/3179100324555214

Possui graduação em Licenciatura em Ciências Biológicas (2011), Mestrado em Ecologia e Biomonitoramento pela Universidade Federal da Bahia (2014) e Doutorado em Ecologia pela UFBA (2019) incluindo Doutorado Sanduíche de um ano no *National Marine Science Centre*, *Southern Cross University*, Austrália. Tem experiência profissional baseada em pesquisa, ensino, extensão na área marinha em temas como, ecologia dos recifes de corais, corais escleractíneos, peixes recifais, espécies exóticas invasoras, áreas marinhas protegidas, mudanças climáticas, delineamento experimental, isótopos estáveis, biomonitoramento, impacto ambiental, serviços ecossistêmicos e áreas afins. Atua em pesquisa há 14 anos utilizando corais, peixes e outras espécies recifais como modelos para avaliação de impacto ambiental tendo publicado 29 artigos e 3 capítulos de livro, alguns de alto impacto. É mergulhador avançado e socorrista certificado pela NAUI com especialidades e técnicas realizadas na Royal Life Saving na Austrália. Atua como revisor de periódicos internacionais como *Proceedings of the Royal Society B*, *Plos One* e *Ecological Indicators* e orienta alunos de graduação e pós-graduação. Já organizou e participou de eventos nacionais e internacionais. Atuou como coordenador de campo pós-doc do projeto Pesquisa Ecológica de Longa Duração (PELD) Costa dos Corais Alagoas na Universidade Federal de Alagoas. Foi pós-doc no Departamento de Biologia Animal na Universidade Federal de Pernambuco, na UFBA/FIOCRUZ desenvolvendo pesquisa em temas como ecologia de micro-organismos e genes resistentes a antibióticos e recente e na UFAL (bolsista PDJ) avaliando o papel de Áreas Marinhas Protegidas e múltiplos impactos sobre a dinâmica funcional e trófica do ecossistema recifal usando corais e peixes como modelo. Atualmente é Professor Visitante no PPG-PROFBIO e desenvolve Pós-Doc no PPG-DIBICT, ambos no Instituto de Ciências Biológicas e da Saúde na UFAL.

José de Anchieta Cintra da Costa Nunes: Lattes – http://lattes.cnpq.br/9034746602077872
Possui graduação em Ciências Biológicas pela Universidade Católica do Salvador (2007). No trabalho de conclusão de curso, estudou assembleias de peixes recifais no Sul da Bahia. Fez Mestrado em Ecologia e Biomonitoramento na Universidade Federal da Bahia (2010-2012, Bolsista CNPq), estudando o papel da complexidade do habitat e exposição de ondas no forrageio e densidades de peixes recifais. O Doutorado em Ecologia na Universidade Federal da Bahia (2013-2017, Bolsista Capes), teve como objetivo entender aspectos da Ecologia do Medo em peixes recifais. Trabalhou com projeto de pós-doutorado na Universidade Federal da Bahia entre 2017-2018 (Bolsista CNPq) e na Universidade Federal do Sul da Bahia (2018-2019, Bolsista da Fundação Renova). Atualmente é Supervisor de Pesquisa do Instituto Meros do Brasil, Equipe Alagoas.

APÊNDICE B – MATERIAL SUPLEMENTAR DO ARTIGO 1

Supplementary Information

Marine Environmental Research

Growth patterns of invasive sun corals can modulate the bioconstruction potential of coral reefs

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Supplementary Information 1 Percentage of benthic coverage at the top of the patches in Cascos Reef (Bahia, Brazil), considering the 46 transects (2017: $n = 26$; 2019: $n = 20$) evaluated using the video-transect (VT) technique. In this study, the analysis of the VTs was performed with the aid of the Video Transect Analyzer software (VTA, Version 1.0, available for download at https://bit.ly/VTA1installer), developed by the Research Group on Coral Reefs and Global Changes (RECOR) of the Federal University of Bahia, from which it was possible to identify aleatory points in a series of consecutive frames directly from the VT, and with that estimate the percentage of benthic coverage (Tables SI 1.1, SI 1.2, and SI 1.3; Fig. SI 1.1 and SI 1.2). The PERMDISP routine was used to test the homogeneity of multivariate dispersions, which showed that the sample dispersion was homogeneous (Table SI 1.4). The SIMPER routine was used to compare which groups and species showed significant changes in benthic cover between 2017 and 2019, which revealed significant mean cover differences for *Tubastraea* sp., crustose coralline algae, and *Madracis decactis* (Table SI 1.5).

Table SI 1.1 Benthic cover (%) at the top of patches in Cascos Reef. Data collection was conducted in February 2017. Abbreviations: MD, *Madracis decatis*; MC, *Montastraea cavernosa*; MHI, *Mussismilia hispida*; SID, *Siderastrea* sp.; TC, *Tubastraea coccinea*; TUB, *Tubastraea* sp.; CAA, Calcareous articulated algae; CCA, Crustose coralline algae; TURF, Turf algae; MAC, Macroalgae; SPO, Sponge; ECH, Echinoderms; SED, Sediment. SD, standard deviation.

Transect	**Corals**								**Algae**						**Others**			
	Natives					**Invaders**			**Calcareous**			**Greens**						
	MC	MD	MHI	SID	**Total**	TC	TUB	**Total**	CAA	CCA	**Total**	TURF	MAC	**Total**	SPO	ECH	SED	**Total**
#1	12.62	0.32	0.63	4.42	**17.99**	0	0.63	**0.63**	30.6	29.97	**60.57**	18.93	0	**18.93**	0.95	0	0.93	**1.88**
#2	20.18	0.3	2.37	3.56	**26.41**	0	0.3	**0.3**	10.98	37.98	**48.96**	24.03	0.3	**24.33**	0	0	0	**0**
#3	18.51	0.3	1.19	1.79	**21.79**	0	2.99	**2.99**	12.84	36.12	**48.96**	24.48	0	**24.48**	1.78	0	0	**1.78**
#4	10.56	0	1.67	1.11	**13.34**	0	2.22	**2.22**	21.94	26.11	**48.05**	34.45	1.94	**36.39**	0	0	0	**0**
#5	3.53	0	0	3.82	**7.35**	0.29	2.06	**2.35**	35.59	29.4	**64.99**	23.53	0	**23.53**	0	0	1.78	**1.78**
#6	3.7	0	1.85	0	**5.55**	1.06	1.59	**2.65**	42.86	28.84	**71.7**	18.52	1.06	**19.58**	0	0.52	0	**0.52**
#7	31.45	0.31	2.52	1.57	**35.85**	0	0	**0**	16.35	27.67	**44.02**	19.81	0.32	**20.13**	0	0	0	**0**
#8	6.11	0	11.67	1.39	**19.17**	0	0	**0**	19.17	38.34	**57.51**	22.78	0.54	**23.32**	0	0	0	**0**
#9	10.81	0	0.68	0.68	**12.17**	0	0.68	**0.68**	24.32	34.12	**58.44**	27.7	1.01	**28.71**	0	0	0	**0**
#10	7.49	2.1	0.3	0	**9.89**	0.6	9.58	**10.18**	26.05	27.25	**53.3**	21.26	0.6	**21.86**	1.48	0	3.29	**4.77**
#11	16.83	0	6.67	1.27	**24.77**	0	0	**0**	1.59	37.46	**39.05**	35.56	0.62	**36.18**	0	0	0	**0**
#12	11.83	0.89	1.18	2.66	**16.56**	0	5.03	**5.03**	23.08	32.54	**55.62**	21.6	0	**21.6**	0.3	0.89	0	**1.19**
#13	19.18	0	0	0	**19.18**	0.63	5.66	**6.29**	19.5	21.7	**41.2**	23.9	1.57	**25.47**	3.46	0	4.4	**7.86**
#14	12.43	0.3	1.78	3.25	**17.76**	0	7.69	**7.69**	19.53	25.74	**45.27**	26.92	0	**26.92**	2.06	0	0.3	**2.36**
#15	16.32	0.53	2.11	4.47	**23.43**	0	5.26	**5.26**	12.89	30.26	**43.15**	28.16	0	**28.16**	0	0	0	**0**
#16	1.89	0	0	0	**1.89**	0	16.4	**16.4**	17.35	29.97	**47.32**	33.44	0.63	**34.07**	0.32	0	0	**0.32**
#17	0.88	0.29	0	0	**1.17**	0	14.71	**14.71**	8.24	28.53	**36.77**	46.17	0.88	**47.05**	0.3	0	0	**0.3**
#18	31.48	0	0	0.28	**31.76**	0	1.11	**1.11**	0.28	34.26	**34.54**	32.31	0.28	**32.59**	0	0	0	**0**

Transect	Corals								Algae						Others			
	Natives					Invaders			Calcareous			Greens						
	MC	MD	MHI	SID	**Total**	TC	TUB	**Total**	CAA	CCA	**Total**	TURF	MAC	**Total**	SPO	ECH	SED	**Total**
#19	20.96	0	0.85	1.7	**23.51**	0	16.71	**16.71**	0.85	26.91	**27.76**	31.73	0.29	**32.02**	0	0	0	**0**
#20	5.03	0.28	1.4	2.51	**9.22**	0	0	**0**	0	44.69	**44.69**	46.09	0	**46.09**	0	0	0	**0**
#21	6.04	0	0	0	**6.04**	0	15.77	**15.77**	2.01	22.14	**24.15**	39.94	13.09	**53.03**	1.01	0	0	**1.01**
#22	21.89	0	0.3	2.96	**25.15**	0	0.59	**0.59**	0	48.82	**48.82**	25.44	0	**25.44**	0	0	0	**0**
#23	10.03	2.36	0	0.29	**12.68**	0	10.32	**10.32**	1.77	33.04	**34.81**	38.94	2.65	**41.59**	0	0	0.6	**0.6**
#24	14.8	1.68	0	0.84	**17.32**	0	2.51	**2.51**	3.07	38.27	**41.34**	36.03	0.84	**36.87**	1.96	0	0	**1.96**
#25	19.06	0	0	0.31	**19.37**	0	0	**0**	3.75	34.07	**37.82**	41.56	0.63	**42.19**	0	0.31	0.31	**0.62**
#26	7.52	0	1.89	4.39	**13.8**	0	0	**0**	3.76	36.99	**40.75**	35.74	9.4	**45.14**	0.31	0	0	**0.31**
Mean	**13.12**	**0.37**	**1.5**	**1.66**	**16.66**	**0.1**	**4.69**	**4.78**	**13.78**	**32.35**	**46.14**	**29.69**	**1.41**	**31.37**	**0.54**	**0.07**	**0.45**	**1.05**
SD	**8.24**	**0.66**	**2.51**	**1.57**	**8.74**	**0.26**	**5.71**	**5.71**	**1.08**	**6.41**	**11.05**	**8.28**	**3.01**	**9.73**	**0.9**	**0.2**	**1.09**	**1.78**

Table SI 1.2 Benthic cover (%) at the top of patches in Cascos Reef. Data collection was conducted in February 2019. Abbreviations: MD, *Madracis decatis*; MC, *Montastraea cavernosa*; MHI, *Mussismilia hispida*; SID, *Siderastrea* sp.; TC, *Tubastraea coccinea*; TUB, *Tubastraea* sp.; CAA, Calcareous articulated algae; CCA, Crustose coralline algae; TURF, Turf algae; MAC, Macroalgae; SPO, Sponge; ECH, Echinoderms; SED, Sediment. SD, standard deviation.

Transect	**Corals**								**Algae**						**Others**			
	Natives					**Invaders**			**Calcareous**			**Greens**						
	MC	MD	MHI	SID	**Total**	TC	TUB	**Total**	CAA	CCA	**Total**	TURF	MAC	**Total**	SPO	ECH	SED	**Total**
#1	0	0	0	0.28	**0.28**	0	18.84	**18.84**	34.07	19.67	**53.74**	26.04	0.82	**26.86**	0	0.28	0	**0.28**
#2	21.23	0	0	2.51	**23.74**	0	17.6	**17.6**	12.85	25.7	**38.55**	19.27	0	**19.27**	0	0	0.84	**0.84**
#3	3.1	1.97	1.97	5.65	**12.69**	0	3.94	**3.94**	21.97	27.32	**49.29**	33.8	0	**33.8**	0	0.28	0	**0.28**
#4	3.27	0.3	0	3.57	**7.14**	0	3.27	**3.27**	17.27	40.77	**58.04**	29.76	0	**29.76**	1.79	0	0	**1.79**
#5	5.03	2.68	0	0	**7.71**	0	15.77	**15.77**	12.42	30.87	**43.29**	32.21	0.67	**32.88**	0.35	0	0	**0.35**
#6	19.75	1.25	0.31	0.31	**21.62**	0	19.13	**19.13**	13.17	24.14	**37.31**	19.75	0	**19.75**	1.88	0.31	0	**2.19**
#7	9.46	4.73	1.26	1.89	**17.34**	0	7.26	**7.26**	5.68	32.49	**38.17**	36.59	0	**36.59**	0.32	0.32	0	**0.64**
#8	6.85	0.93	0	2.49	**10.27**	0	22.74	**22.74**	12.15	22.74	**34.89**	29.28	0.31	**29.59**	2.2	0	0.31	**2.51**
#9	8.2	0.63	0.32	0.63	**9.78**	0	14.51	**14.51**	9.78	26.5	**36.28**	39.12	0	**39.12**	0	0	0.31	**0.31**
#10	33.23	0	0	0.89	**34.12**	0	4.45	**4.45**	16.32	23.74	**40.06**	20.77	0	**20.77**	0.6	0	0	**0.6**
#11	15.51	0.63	0.95	1.9	**18.99**	0	0.63	**0.63**	11.71	31.65	**43.36**	35.13	0.63	**35.76**	1.26	0	0	**1.26**
#12	2.31	0	0	0.77	**3.08**	0	0	**0**	13.46	22.31	**35.77**	54.23	6.92	**61.15**	0	0	0	**0**
#13	4.09	0	0.63	0.64	**5.36**	0	15.72	**15.72**	29.25	22.74	**51.99**	26.1	0	**26.1**	0.83	0	0	**0.83**
#14	8.2	0.32	0	0	**8.52**	4.73	19.87	**24.6**	24.92	17.98	**42.9**	21.77	0	**21.77**	1.89	0.32	0	**2.21**
#15	4.68	2.34	0	0	**7.02**	0	5.35	**5.35**	26.42	23.08	**49.5**	37.46	0	**37.46**	0.67	0	0	**0.67**
#16	5.35	0	0	0	**5.35**	0	29.77	**29.77**	12.71	31.44	**44.15**	20.4	0	**20.4**	0.33	0	0	**0.33**
#17	18.82	0	0	1.76	**20.58**	0	2.94	**2.94**	27.94	29.41	**57.35**	19.13	0	**19.13**	0	0	0	**0**
#18	9.75	4.69	0	0.72	**15.16**	0	22.02	**22.02**	24.19	18.05	**42.24**	20.58	0	**20.58**	0	0	0	**0**

Transect	Corals								Algae						Others			
	Natives					Invaders			Calcareous			Greens						
	MC	MD	MHI	SID	**Total**	TC	TUB	**Total**	CAA	CCA	**Total**	TURF	MAC	**Total**	SPO	ECH	SED	**Total**
#19	15.31	0.31	0.31	0.94	**16.87**	0	16.88	**16.88**	15.94	25	**40.94**	19.38	5.3	**24.68**	0.63	0	0	**0.63**
#20	11.37	1.34	0.33	2.34	**15.38**	0	3.68	**3.68**	26.1	21.4	**47.5**	32.44	1	**33.44**	0	0	0	**0**
Mean	**10.28**	**1.11**	**0.3**	**1.36**	**13.05**	**0.24**	**1.22**	**12.46**	**18.42**	**25.85**	**44.27**	**28.66**	**0.78**	**29.44**	**0.64**	**0.08**	**0.07**	**0.79**
SD	**8.19**	**1.48**	**0.53**	**1.44**	**8.23**	**1.06**	**8.79**	**9.07**	**7.78**	**5.62**	**7.08**	**9.18**	**1.87**	**10.10**	**0.76**	**0.13**	**0.2**	**0.79**

Fig. SI 1.1 Variation of benthic cover (%) in each of the 26 transects evaluated at the top of the patches in Recife dos Cascos in 2017. Abbreviations: MD, *Madracis decatis*; MC, *Montastraea cavernosa*; MHI, *Mussismilia hispida*; SID, *Siderastrea* sp.; TC, *Tubastraea coccinea*; TUB, *Tubastraea* sp.; CAA, Calcareous articulated algae; CCA, Crustose coralline algae; TURF, Turf algae; MAC, Macroalgae; SPO, Sponge; ECH, Echinoderms; SED, Sediment.

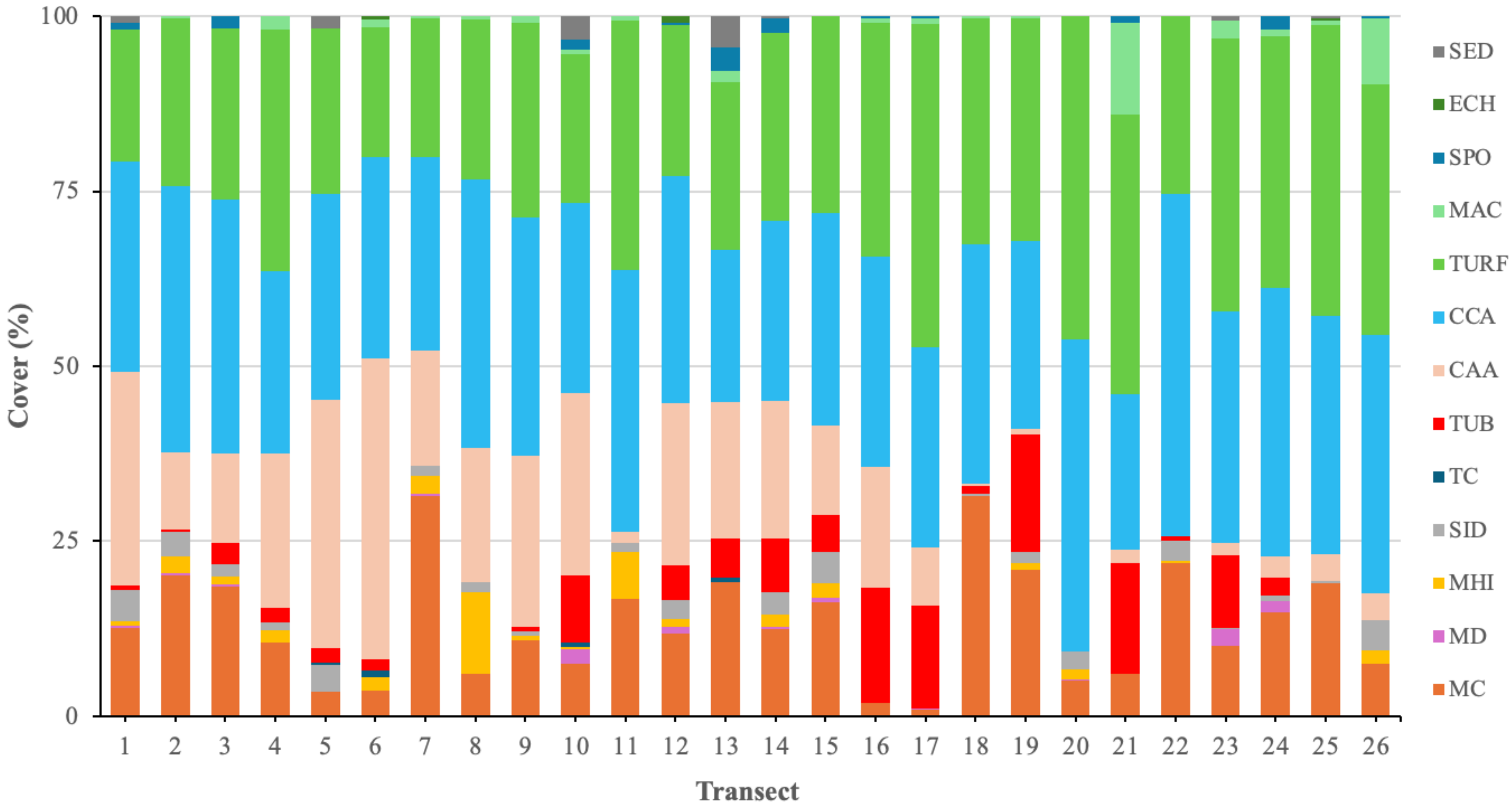

Fig. SI 1.2 Variation of benthic cover (%) in each of the 20 transects evaluated at the top of the patches in Recife dos Cascos in 2019. Abbreviations: MD, *Madracis decatis*; MC, *Montastraea cavernosa*; MHI, *Mussismilia hispida*; SID, *Siderastrea* sp.; TC, *Tubastraea coccinea*; TUB, *Tubastraea* sp.; CAA, Calcareous articulated algae; CCA, Crustose coralline algae; TURF, Turf algae; MAC, Macroalgae; SPO, Sponge; ECH, Echinoderms; SED, Sediment.

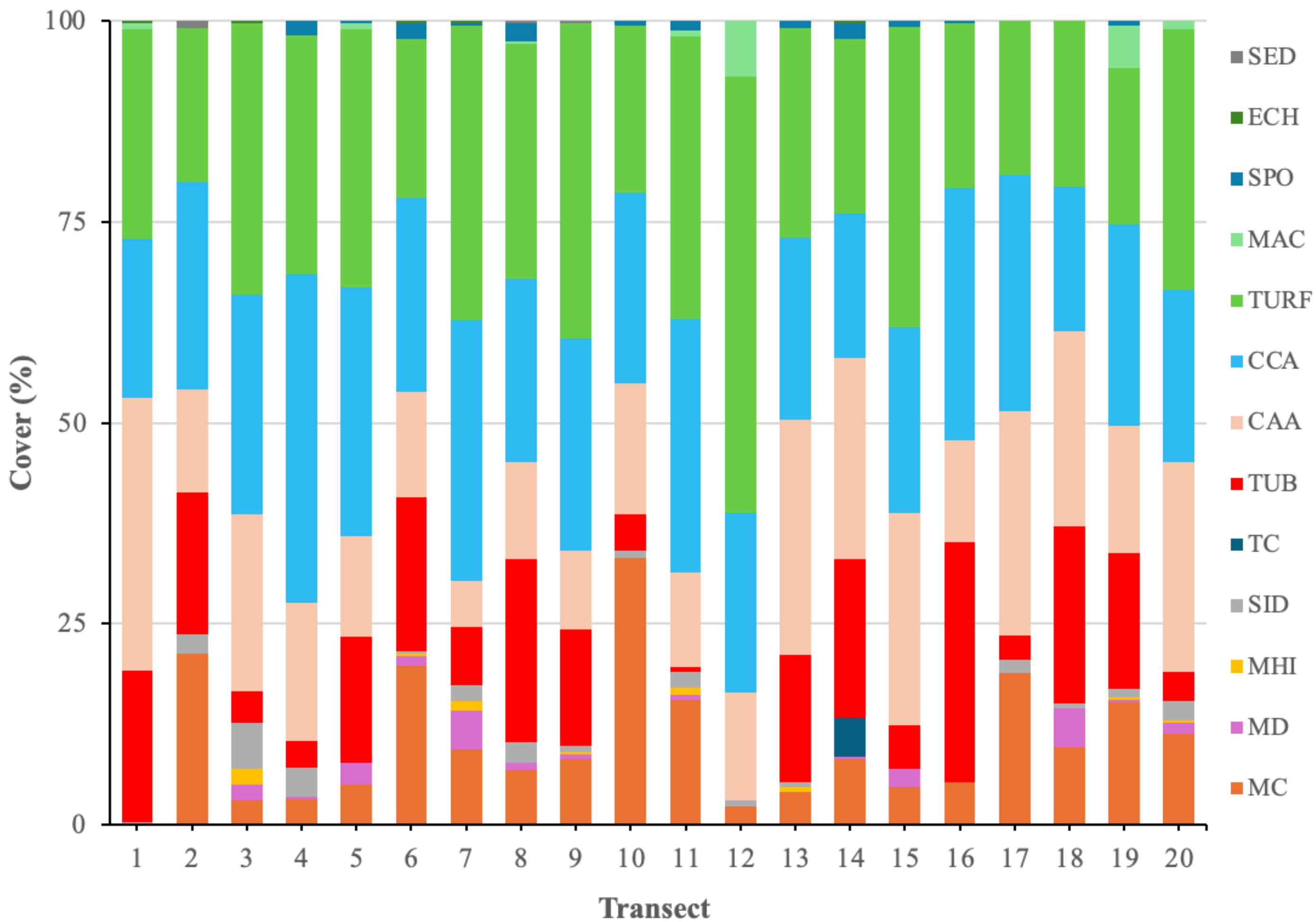

Table SI 1.3 Mean coral cover (%) at the top of patches in Cascos Reef, considering the campaigns conducted in 2017 and 2019.

Corals, mean ± SD: 23.21 ± 9.33%								
Group	**Natives**					**Invaders**		
Specie	MC	MD	MHI	SID	**Total**	TC	TUB	**Total**
Mean ± SD	11.88 ± 8.25	0.69 ± 1.14	0.98 ± 2.00	1.53 ± 1.51	**15.09 ± 8.62**	0.16 ± 0.72	7.96 ± 8.06	**8.12 ± 8.22**

Table SI 1.4 PERMDISP test of the benthic assemblage (percentage cover) considering the group "Year".

Group	DF	MS	*F*	*P*
Year (2017-2019)	1	0.0020	0.6756	0.4155
Residuals	44	0.1280	0.0029	

Table SI 1.5 SIMPER output for "Year" of the benthic assemblage (percentage cover).

Benthic group	2017[a]	2019[a]	Av. Diss.	Diss./SD	Contrib. %	Cum. %	*P*
CAA	13.78	18.42	0.0615	0.0413	21.30	21.30	0.2069
TUB	4.68	12.22	0.0509	0.0381	17.60	38.90	0.0009***
TURF	29.96	28.66	0.0482	0.0370	16.70	55.60	0.5429
MC	13.12	10.28	0.0461	0.0361	16.00	71.60	0.4092
CCA	32.35	25.85	0.0429	0.0310	14.90	86.50	0.0014**
MAC	1.41	0.78	0.0090	0.0152	3.10	89.60	0.6241
SID	1.66	1.36	0.0082	0.0066	2.80	92.40	0.7608
MHI	1.50	0.30	0.0074	0.0119	2.60	95.00	0.4868
MD	0.37	1.11	0.0057	0.0067	2.00	97.00	0.0184*
SPO	0.54	0.64	0.0041	0.0049	1.40	98.40	0.5225
SED	0.45	0.07	0.0025	0.0052	0.80	99.20	0.9675
TC	0.10	0.24	0.0016	0.0051	0.60	99.80	0.3884
ECH	0.07	0.08	0.0006	0.0010	0.20	100.00	0.3744

[a] Percentage of coverage of benthic groups. Abbreviations: MC, *Montastraea cavernosa*; MD, *Madracis decatis*; MHI, *Mussismilia hispida*; *Siderastrea* sp.; TC, *Tubastraea coccinea*; TUB, *Tubastraea* sp.; CAA, Calcareous articulated algae; CCA, Crustose coralline algae; TURF, Turf algae; MAC, Macroalgae; SPO, Sponge; ECH, Echinoderms; SED, Sediment. Significant at 0.05 level (*); Significant at 0.01 level (**); Significant at 0.001 level (***).

Supplementary Information 2 Three growth parameters were calculated for the evaluated coral species. Skeletal extension (cm y^{-1}) rate was measured using the Alizarin staining technique and direct measurements for *Tubastraea* sp. and *T. coccinea*. X-ray techniques and measurements of the density bands' linear extension were used to determine the skeletal extension rate of *M. cavernosa*. For *Siderastrea* sp., the skeletal extension rate was estimated through alizarin staining evidence observed in the skeleton surface areas. Bulk skeletal density (g cm^{-3}) was determined using Archimedes' principle. The calcification rate (g cm^{-2} y^{-1}) was calculated as a function of the skeletal extension rate, bulk density and an adjustment coefficient (0 = no growth, 1 = continuous growth surface)

Table SI 2.1 Skeletal extension (cm y^{-1}), bulk skeletal density (g cm^{-3}), and calcification rate (g cm^{-2} y^{-1}) of invasive corals at Cascos Reef, Brazil. Growth parameter values of species and samples are presented as mean ± standard deviation (minimum-maximum).

Specie, sample and subsample	**Growth morphology**	**Skeletal extension (cm y^{-1})**	**Bulk skeletal density (g cm^{-3})**	**Adjustment coefficient**	**Calcification rate (g cm^{-2} y^{-1})**
***Tubastraea* sp.**	**Dendroid**	**0.48 ± 0.13 (0.32–0.70)[a]**	**1.39 ± 0.06 (1.27–1.47)**	**0.4**	**0.26 ± 0.03 (0.22–0.31)**
TUB 01		0.54 ± 0.13 (0.35–0.70)	1.42 ± 0.03 (1.39–1.46)		0.30 ± 0.01 (0.30–0.31)
A			1.40		0.30
B			1.41		0.30
C			1.46		0.31
TUB 02		0.45 ± 0.07 (0.39–0.55)	1.43 ± 0.05 (1.38–1.47)		0.26 ± 0.01 (0.25–0.26)
A			1.44		0.26
B			1.38		0.25
C			1.47		0.26
TUB 03		0.48 ± 0.12 (0.36–0.66)	1.35 ± 0.09 (1.27–1.44)		0.26 ± 0.02 (0.24–0.28)
A			1.44		0.28
B			1.34		0.26
C			1.27		0.24
TUB 04		0.41 ± 0.16 (0.32–0.65)	1.37 ± 0.07 (1.33–1.45)		0.23 ± 0.01 (0.22–0.24)
A			1.35		0.22
B			1.33		0.22
C			1.45		0.24

Specie, sample and subsample	Growth morphology	Skeletal extension (cm y^{-1})	Bulk skeletal density (g cm^{-3})	Adjustment coefficient	Calcification rate (g cm^{-2} y^{-1})
Tubastraea coccinea	**Plocoid**	**0.27 ± 0.09 (0.15–0.42)[a]**	**1.07 ± 0.04 (1.01–1.14)**	**0.4**	**0.12 ± 0.03 (0.09–0.16)**
TC 01		0.22 ± 0.07 (0.17–0.33)	1.10 ± 0.03 (1.08–1.13)		0.10 ± 0.01 (0.09–0.10)
A			1.08		0.09
B			1.08		0.10
C			1.13		0.10
TC 02		0.21 ± 0.06 (0.15–0.30)	1.05 ± 0.04 (1.02–1.10)		0.09 ± 0.01 (0.09–0.09)
A			1.10		0.09
B			1.02		0.09
C			1.04		0.09
TC 03		0.38 ± 0.04 (0.33–0.42)	1.04 ± 0.01 (1.03–1.05)		0.16 ± 0.01 (0.16–0.16)
A			1.03		0.16
B			1.04		0.16
C			1.05		0.16
TC 04		0.27 ± 0.07 (0.20–0.36)	1.09 ± 0.07 (1.01–1.14)		0.12 ± 0.01 (0.11–0.12)
A			1.11		0.12
B			1.01		0.11
C			1.14		0.12

[a] Alizarin staining and direct measurements.

Table SI 2.2 Skeletal extension (cm y^{-1}), bulk skeletal density (g cm^{-3}), and calcification (g cm^{-2} y^{-1}) of native corals at Cascos Reef, Brazil. Growth parameter values of species and samples are presented as mean ± standard deviation (minimum-maximum).

Specie, sample and subsample	**Growth morphology**	**Skeletal extension (cm y^{-1})**	**Bulk skeletal density (g cm^{-3})**	**Adjustment coefficient**	**Calcification rate (g cm^{-2} y^{-1})**
Montastraea cavernosa	**Massive**	**0.15 ± 0.04 (0.08–0.24)**[a]	**1.71 ± 0.17 (1.54–1.95)**	**1**	**0.26 ± 0.02 (0.23–0.29)**
MC 01		0.16 ± 0.03 (0.08–0.22)	1.63 ± 0.05 (1.601.69)		0.26 ± 0.01 (0.25–0.27)
A			1.69		0.27
B			1.60		0.26
C			1.62		0.26
MC 02		0.15 ± 0.04 (0.10–0.24)	1.79 ± 0.22 (1.54–1.95)		0.27 ± 0.03 (0.23–0.29)
A			1.95		0.29
B			1.54		0.23
C			1.89		0.28
***Siderastrea* sp.**	**Massive**	**0.10 ± 0.05 (0.00–0.15)**[b]	**1.62 ± 0.07 (1.51–1.69)**	**1**	**0.17 ± 0.01 (0.16–0.17)**
SID 01		0.1 ± 0.05 (0.00–0.15)	1.62 ± 0.06 (1.55–1.67)		0.17 ± 0.01 (0.16–0.17)
A			1.67		0.17
B			1.64		0.17
C			1.55		0.16
SID 02		0.1 ± 0.05 (0.00–0.15)	1.63 ± 0.10 (1.51–1.69)		0.17 ± 0.01 (0.16–0.17)
A			1.68		0.17
B			1.69		0.17
C			1.51		0.16

[a] X-radiography and density bands. [b] Estimate from alizarin staining evidence, X-radiography, and density bands.

Supplementary Information 3 Coral carbonate production (kg $CaCO_3$ m^{-2} y^{-1}) was calculated as a function of substrate area occupied by each coral species (i.e., mean percent cover), their skeletal extension (cm y^{-1}), and bulk density (g cm^{-3}). For this, we utilized the ReefBudget methodology (adapted), which focuses on quantifying the relative contributions of different carbonate producer groups to biologically driven carbonate production. The equations for calculate the coral growth parameters were applied to yield a value for coral carbonate production relative to the actual transect surface areas evaluated. Differences in coral carbonate production rates (intra-specific, intra-cluster, and interannual) were evaluated using the Kruskal-Wallis and Mann-Whitney non-parametric tests. *Post-hoc* Dunn's tests were employed for all pairwise comparisons when necessary.

Table SI 3.1 Substrate area occupied (m^2) by corals (native and invasive species) and their carbonate production rate (kg $CaCO_3$ m^{-2} y^{-1}) at the top of patches in Cascos Reef in 2017.

Transect	Substrate area occupied (m^2)						Carbonate production rate (kg $CaCO_3$ m^{-2} y^{-1})						
	Natives			Invaders			Natives			Invaders			Transect[a]
	MC	SID	**Total**	TUB	TC	**Total**	MC	SID	**Total**	TUB	TC	**Total**	
#1	0.38	0.13	**0.51**	0.02	0	**0.02**	1.00	0.22	**1.22**	0.05	0	**0.05**	1.27
#2	0.61	0.11	**0.71**	0.01	0	**0.01**	1.60	0.18	**1.77**	0.02	0	**0.02**	1.80
#3	0.56	0.05	**0.61**	0.09	0	**0.09**	1.46	0.09	**1.55**	0.23	0	**0.23**	1.79
#4	0.32	0.03	**0.35**	0.07	0	**0.07**	0.84	0.06	**0.89**	0.17	0	**0.17**	1.06
#5	0.11	0.11	**0.22**	0.06	0.01	**0.07**	0.28	0.19	**0.47**	0.16	0.01	**0.17**	0.64
#6	0.11	0	**0.11**	0.05	0.03	**0.08**	0.29	0	**0.29**	0.12	0.04	**0.16**	0.45
#7	0.94	0.05	**0.99**	0.00	0	**0.00**	2.49	0.08	**2.57**	0	0	**0**	2.57
#8	0.18	0.04	**0.23**	0.00	0	**0.00**	0.48	0.07	**0.55**	0	0	**0**	0.55
#9	0.32	0.02	**0.34**	0.02	0	**0.02**	0.86	0.03	**0.89**	0.05	0	**0.05**	0.94
#10	0.22	0	**0.22**	0.29	0.02	**0.31**	0.59	0	**0.59**	0.75	0.02	**0.77**	1.37
#11	0.50	0.04	**0.54**	0.00	0	**0.00**	1.33	0.06	**1.39**	0	0	**0**	1.39
#12	0.35	0.08	**0.43**	0.15	0	**0.15**	0.94	0.13	**1.07**	0.39	0	**0.39**	1.46
#13	0.58	0	**0.58**	0.17	0.02	**0.19**	1.52	0	**1.52**	0.44	0.02	**0.47**	1.98
#14	0.37	0.10	**0.47**	0.23	0	**0.23**	0.98	0.16	**1.14**	0.60	0	**0.60**	1.75
#15	0.49	0.13	**0.62**	0.16	0	**0.16**	1.29	0.22	**1.51**	0.41	0	**0.41**	1.93
#16	0.06	0	**0.06**	0.49	0	**0.49**	0.15	0	**0.15**	1.29	0	**1.29**	1.44
#17	0.03	0	**0.03**	0.44	0	**0.44**	0.07	0	**0.07**	1.15	0	**1.15**	1.22
#18	0.94	0.01	**0.95**	0.03	0	**0.03**	2.49	0.01	**2.50**	0.09	0	**0.09**	2.59

Transect	Substrate area occupied (m^2)						Carbonate production rate (kg $CaCO_3$ m^{-2} y^{-1})						
	Natives			Invaders			Natives			Invaders			Transect[a]
	MC	SID	**Total**	TUB	TC	**Total**	MC	SID	**Total**	TUB	TC	**Total**	
#19	0.63	0.05	**0.68**	0.50	0	**0.50**	1.66	0.08	**1.74**	1.31	0	**1.31**	3.05
#20	0.15	0.08	**0.23**	0.00	0	**0.00**	0.40	0.12	**0.52**	0	0	**0**	0.52
#21	0.18	0	**0.18**	0.47	0	**0.47**	0.48	0	**0.48**	1.24	0	**1.24**	1.72
#22	0.66	0.09	**0.75**	0.02	0	**0.02**	1.73	0.15	**1.88**	0.05	0	**0.05**	1.92
#23	0.30	0.01	**0.31**	0.31	0	**0.31**	0.79	0.01	**0.81**	0.81	0	**0.81**	1.62
#24	0.44	0.03	**0.47**	0.08	0	**0.08**	1.17	0.04	**1.21**	0.20	0	**0.20**	1.41
#25	0.57	0.01	**0.58**	0.00	0	**0.00**	1.51	0.02	**1.52**	0	0	**0**	1.52
#26	0.23	0.13	**0.36**	0.00	0	**0.00**	0.59	0.22	**0.81**	0	0	**0**	0.81
Mean	**0.39**	**0.05**	**0.44**	**0.14**	**0.00**	**0.14**	**1.04**	**0.08**	**1.12**	**0.37**	**0.00**	**0.37**	**1.49**
SD	**0.25**	**0.05**	**0.26**	**0.17**	**0.01**	**0.17**	**0.65**	**0.08**	**0.66**	**0.45**	**0.01**	**0.45**	**0.65**

[a] Transect carbonate production rate was estimated considering only the mentioned coral species (natives and invaders). MC, *Montastraea cavernosa*; *Siderastrea* sp.; TUB, *Tubastraea* sp., TC, *Tubastraea coccinea*. SD, standard deviation.

Table SI 3.2 Substrate area occupied (m^2) by corals (native and invasive species) and their carbonate production rate (kg $CaCO_3$ m^{-2} y^{-1}) at the top of patches in Cascos Reef in 2019.

Transect	**Substrate area occupied (m^2)**						**Carbonate production rate (kg $CaCO_3$ m^{-2} y^{-1})**						
	Natives			**Invaders**			**Natives**			**Invaders**			**Transect**[a]
	MC	SID	**Total**	TUB	TC	**Total**	MC	SID	**Total**	TUB	TC	**Total**	
#1	0	0.01	**0.01**	0.57	0	**0.57**	0	0.01	**0.01**	1.48	0	**1.48**	1.49
#2	0.64	0.08	**0.71**	0.53	0	**0.53**	1.68	0.12	**1.80**	1.38	0	**1.38**	3.19
#3	0.09	0.17	**0.26**	0.12	0	**0.12**	0.25	0.28	**0.53**	0.31	0	**0.31**	0.84
#4	0.10	0.11	**0.21**	0.10	0	**0.10**	0.26	0.18	**0.44**	0.26	0	**0.26**	0.69
#5	0.15	0	**0.15**	0.47	0	**0.47**	0.40	0	**0.40**	1.24	0	**1.24**	1.64
#6	0.59	0.01	**0.60**	0.57	0	**0.57**	1.56	0.02	**1.58**	1.50	0	**1.50**	3.08
#7	0.28	0.06	**0.34**	0.22	0	**0.22**	0.75	0.09	**0.84**	0.57	0	**0.57**	1.41
#8	0.21	0.07	**0.28**	0.68	0	**0.68**	0.54	0.12	**0.67**	1.79	0	**1.79**	2.45
#9	0.25	0.02	**0.26**	0.44	0	**0.44**	0.65	0.03	**0.68**	1.14	0	**1.14**	1.82
#10	1.00	0.03	**1.02**	0.13	0	**0.13**	2.63	0.04	**2.67**	0.35	0	**0.35**	3.02
#11	0.47	0.06	**0.52**	0.02	0	**0.02**	1.23	0.09	**1.32**	0.05	0	**0.05**	1.37
#12	0.07	0.02	**0.09**	0	0	**0**	0.18	0.04	**0.22**	0	0	**0**	0.22
#13	0.12	0.02	**0.14**	0.47	0	**0.47**	0.32	0.03	**0.36**	1.23	0	**1.23**	1.59
#14	0.25	0	**0.25**	0.60	0.14	**0.74**	0.65	0	**0.65**	1.56	0.16	**1.72**	2.37
#15	0.14	0	**0.14**	0.16	0	**0.16**	0.37	0	**0.37**	0.42	0	**0.42**	0.79
#16	0.16	0	**0.16**	0.89	0	**0.89**	0.42	0	**0.42**	2.34	0	**2.34**	2.79
#17	0.56	0.05	**0.62**	0.09	0	**0.09**	1.49	0.09	**1.58**	0.23	0	**0.23**	1.81
#18	0.29	0.02	**0.31**	0.66	0	**0.66**	0.77	0.04	**0.81**	1.73	0	**1.73**	2.54

Transect	Substrate area occupied (m^2)						Carbonate production rate (kg $CaCO_3$ m^{-2} y^{-1})						
	Natives			Invaders			Natives			Invaders			Transect[a]
	MC	SID	**Total**	TUB	TC	**Total**	MC	SID	**Total**	TUB	TC	**Total**	
#19	0.46	0.03	**0.49**	0.51	0	**0.51**	1.21	**0.05**	1.26	1.33	0	**1.33**	2.58
#20	0.34	0.07	**0.41**	0.11	0	**0.11**	0.90	**0.12**	1.02	0.29	0	**0.29**	1.30
Mean	**0.31**	**0.04**	**0.35**	**0.37**	**0.01**	**0.37**	**0.81**	**0.07**	**0.88**	**0.96**	**0.01**	**0.97**	**1.85**
SD	**0.25**	**0.04**	**0.25**	**0.26**	**0.03**	**0.27**	**0.65**	**0.07**	**0.65**	**0.69**	**0.04**	**0.70**	**0.87**

[a] Transect carbonate production rate was estimated considering only the mentioned coral species (natives and invaders). Abbreviations: MC, *Montastraea cavernosa*; SID, *Siderastrea* sp.; TUB, *Tubastraea* sp., TC, *Tubastraea coccinea*. SD, standard deviation.

Table SI 3.3 Inter-specific and inter-cluster comparisons of carbonate production rates using the Kruskal-Wallis test followed by Dunn's post-hoc and the Mann-Whitney, respectively.

Pair-wise comparison	Inter-specific			Comparison	Inter-cluster		
	Z	***P*[a]**			***W***	***P***	
MC-SID	-6.33	<0.0001	****	Native-Invasive	1466.5	0.0014	**
MC-TC	-9.98	<0.0001	****				
MC-TUB	-2.47	0.0812	ns				
SID-TC	-3.65	0.0016	**				
SID-TUB	3.86	0.0007	***				
TC-TUB	7.51	<0.0001	****				

Abbreviations: MC, *Montastraea cavernosa*; SID, *Siderastrea* sp., TUB, *Tubastraea* sp.; TC, *Tubastraea coccinea*. [a] Adjusted for Bonferroni correction at the 95% confidence level. Significance levels: * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$), **** ($P < 0.0001$); ns indicates not significant at $P < 0.05$.

Table SI 3.4 Inter-annual comparisons results (2017 vs 2019) of carbonate production rate using a Mann-Whitney test.

Comparison	Intra-specific			Comparison	Intra-cluster			Comparison	Between years		
	W	***P***			***W***	***P***			***W***	***P***	
MC	320.5	0.1836	ns	Native	319	0.1948	ns	2017-2019	3692	0.1847	ns
SID	281.5	0.6395	ns	Invasive	3430	0.0259	*				
TC	285	0.315	ns								
TUB	115.5	0.0014	**								

Abbreviations: MC, *Montastraea cavernosa*; SID, *Siderastrea* sp., TUB, *Tubastraea* sp.; TC, *Tubastraea coccinea*. Significance levels: * ($P < 0.05$), ** ($P < 0.01$); ns indicates not significant at $P < 0.05$.

APÊNDICE C – MATERIAL SUPLEMENTAR DO ARTIGO 2

Supplementary Information

Marine Biology

International Journal on Life in Oceans and Coastal Waters

Effects of invasive sun corals on habitat structural complexity mediate reef trophic pathways

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Supplementary Information 1 Spearman correlation test between each of the environmental predictors

We evaluated the correlation between each predictor using the Spearman correlation coefficient (r), whose values can vary between -1 (inverse relationships) and +1. Thus, the values indicate the magnitude of the correlation between the variables, which can be classified as “weak” (0.1 < | r | < 0.39), “moderate” (0.39 < | r | < 0.69) or “strong” (0.70 < | r | < 1.00) (Burnham and Anderson 2004). In our study, we created Generalized Linear Models to evaluate the effect of predictor variables on the abundance of fish trophic groups in Cascos Reef (Bahia, Brazil), which showed Spearman correlation values lower than 0.70 (Table SI 1).

Table SI 1 Correlation between the different environmental predictor variables used in this study. Values presented refer to the Spearman correlation coefficient (r). CAA, Calcareous articulated algae; CCA, Crustose coralline algae; TURF, Turf algae; MAC, Macroalgae; CCI_{Native}, Contribution index of native corals to reef complexity; $CCI_{Invader}$, Contribution index of invasive corals to reef complexity; and DRR_{STD}, Digital rugosity.

	CAA	**CCA**	**TURF**	**MAC**	**CCI_{Native}**	**$CCI_{Invader}$**	**DRR_{STD}**
CAA		-0.44	-0.33	0.00	0.13	-0.14	-0.06
CCA	-0.44		-0.11	-0.23	-0.16	0.13	0.17
TURF	-0.33	-0.11		0.40	-0.21	-0.53	-0.19
MAC	0.00	-0.23	0.40		0.10	-0.54	-0.50
CCI_{Native}	0.13	-0.16	-0.21	0.10		-0.32	-0.10
$CCI_{Invader}$	-0.14	0.13	-0.53	-0.54	-0.32		0.45
DRR_{STD}	-0.06	0.17	-0.19	-0.50	-0.10	0.45	

References Supplementary Information 1

Schober P, Boer C, Schwarte LA (2018) Correlation Coefficients: Appropriate Use and Interpretation. Anesth Analg 126:1763–1768

Supplementary Information 2 Percentage of benthic coverage at the top of the patches in Cascos Reef (Bahia, Brazil), considering the 40 transects evaluated using the video-transect (VT) technique. In this study, the analysis of the VTs was performed with the aid of the Video Transect Analyzer software (Version 1.0), developed by the Research Group on Coral Reefs and Global Changes (RECOR) of the Federal University of Bahia, from which it was possible to identify aleatory points in a series of consecutive frames directly from the VT, and with that estimate the percentage of benthic coverage (Tables SI 2.1 and SI 2.2; Fig. SI 2.1). We used Principal Component Analysis (PCA) to characterize possible relationships between the main benthic groups, which showed negative covariance both between the cover of the invasive coral Tubastraea sp. and turf algae and between crustose coralline algae and calcareous articulated algae. The first two axes explained 61.8% of the total variance of the benthic cover at the top of the patches in Cascos Reef (Fig. SI 2.2).

Table SI 2.1 Benthic cover (%) at the top of patches in Cascos Reef. MD, *Madracis decactis*; MC, *Montastraea cavernosa*; MHI, *Mussismilia hispida*; SID, *Siderastrea* sp.; TC, *Tubastraea coccinea*; TUB, *Tubastraea* sp.; CAA, Calcareous articulated algae; CCA, Crustose coralline algae; TURF, Turf algae; MAC, Macroalgae; SPO, Sponge; ECH, Echinoderms; SED, Sediment.

Transect	Corals								Algae						Other			
	Natives					Invaders			Calcareous			Greens						
	MD	MC	MHI	SID	**Total**	TC	TUB	**Total**	CAA	CCA	**Total**	TURF	MAC	**Total**	SPO	ECH	SED	**Total**
1	0	0	0	0.28	**0.28**	0	18.84	**18.84**	34.07	19.67	**53.74**	26.04	0.82	**26.86**	0	0.28	0	**0.28**
2	0	21.23	0	2.51	**23.74**	0	17.6	**17.6**	12.85	25.7	**38.55**	19.27	0	**19.27**	0	0	0.84	**0.84**
3	1.97	3.1	1.97	5.65	**12.69**	0	3.94	**3.94**	21.97	27.32	**49.29**	33.8	0	**33.8**	0	0.28	0	**0.28**
4	0.3	3.27	0	3.57	**7.14**	0	3.27	**3.27**	17.27	40.77	**58.04**	29.76	0	**29.76**	1.79	0	0	**1.79**
5	2.68	5.03	0	0	**7.71**	0	15.77	**15.77**	12.42	30.87	**43.29**	32.21	0.67	**32.88**	0.35	0	0	**0.35**
6	1.25	19.75	0.31	0.31	**21.62**	0	19.13	**19.13**	13.17	24.14	**37.31**	19.75	0	**19.75**	1.88	0.31	0	**2.19**
7	4.73	9.46	1.26	1.89	**17.34**	0	7.26	**7.26**	5.68	32.49	**38.17**	36.59	0	**36.59**	0.32	0.32	0	**0.64**
8	0.93	6.85	0	2.49	**10.27**	0	22.74	**22.74**	12.15	22.74	**34.89**	29.28	0.31	**29.59**	2.2	0	0.31	**2.51**
9	0.63	8.2	0.32	0.63	**9.78**	0	14.51	**14.51**	9.78	26.5	**36.28**	39.12	0	**39.12**	0	0	0.32	**0.32**
10	0	33.23	0	0.89	**34.12**	0	4.45	**4.45**	16.32	23.74	**40.06**	20.77	0	**20.77**	0.59	0	0	**0.59**
11	0.63	15.51	0.95	1.9	**18.99**	0	0.63	**0.63**	11.71	31.65	**43.36**	35.13	0.63	**35.76**	1.27	0	0	**1.27**
12	0	2.31	0	0.77	**3.08**	0	0	**0**	13.46	22.31	**35.77**	54.23	6.92	**61.15**	0	0	0	**0**
13	0	4.09	0.63	0.64	**5.36**	0	15.72	**15.72**	29.25	22.74	**51.99**	26.1	0	**26.1**	0.83	0	0	**0.83**
14	0.32	8.2	0	0	**8.52**	4.73	19.87	**24.6**	24.92	17.98	**42.9**	21.77	0	**21.77**	1.89	0.32	0	**2.21**
15	2.34	4.68	0	0	**7.02**	0	5.35	**5.35**	26.42	23.08	**49.5**	37.46	0	**37.46**	0.67	0	0	**0.67**
16	0	5.35	0	0	**5.35**	0	29.77	**29.77**	12.71	31.44	**44.15**	20.4	0	**20.4**	0.33	0	0	**0.33**
17	0	18.82	0	1.76	**20.58**	0	2.94	**2.94**	27.94	29.41	**57.35**	19.13	0	**19.13**	0	0	0	**0**
18	4.69	9.75	0	0.72	**15.16**	0	22.02	**22.02**	24.19	18.05	**42.24**	20.58	0	**20.58**	0	0	0	**0**
19	0.31	15.31	0.31	0.94	**16.87**	0	16.88	**16.88**	15.94	25	**40.94**	19.38	5.3	**24.68**	0.63	0	0	**0.63**
20	1.34	11.37	0.33	2.34	**15.38**	0	3.68	**3.68**	26.1	21.4	**47.5**	32.44	1	**33.44**	0	0	0	**0**

Table SI 2.1 Continued Benthic cover (%) at the top of patches in Cascos Reef. MD, *Madracis decactis*; MC, *Montastraea cavernosa*; MHI, *Mussismilia hispida*; SID, *Siderastrea* sp.; TC, *Tubastraea coccinea*; TUB, *Tubastraea* sp.; CAA, Calcareous articulated algae; CCA, Crustose coralline algae; TURF, Turf algae; MAC, Macroalgae; SPO, Sponge; ECH, Echinoderms; SED, Sediment.

Transect	**Corals**								**Algae**						**Other**			
	Natives					**Invaders**			**Calcareous**			**Greens**						
	MD	MC	MHI	SID	**Total**	TC	TUB	**Total**	CAA	CCA	**Total**	TURF	MAC	**Total**	SPO	ECH	SED	**Total**
21	0	22.85	0	1.19	**24.04**	0	0	**0**	15.73	24.04	**39.77**	34.41	1.48	**35.89**	0.3	0	0	**0.3**
22	0	11.31	2.08	1.49	**14.88**	0	0	**0**	19.05	20.54	**39.59**	45.53	0	**45.53**	0	0	0	**0**
23	0	18.61	3.79	2.21	**24.61**	0	0	**0**	6.31	34.06	**40.37**	34.7	0.32	**35.02**	0	0	0	**0**
24	6.05	11.58	2.63	2.63	**22.89**	0	0.53	**0.53**	23.68	30	**53.68**	22.9	0	**22.9**	0	0	0	**0**
25	0	11.73	0	0.84	**12.57**	0	0	**0**	17.6	33.8	**51.4**	31.56	3.35	**34.91**	0.84	0.28	0	**1.12**
26	0	12.01	2.23	3.91	**18.15**	0	0	**0**	37.43	15.31	**52.74**	27.09	1.68	**28.77**	0.34	0	0	**0.34**
27	0	2.96	0.59	2.07	**5.62**	0	0.3	**0.3**	22.49	23.31	**45.8**	42.01	2.66	**44.67**	0.95	0	2.66	**3.61**
28	0	6.53	4.63	1.05	**12.21**	0	0	**0**	31.79	22.95	**54.74**	25.68	7.37	**33.05**	0	0	0	**0**
29	0.6	7.19	0	0.6	**8.39**	0	0	**0**	16.17	29.34	**45.51**	42.8	1.8	**44.6**	1.5	0	0	**1.5**
30	0	19.8	5.03	2.68	**27.51**	0	0	**0**	9.73	22.15	**31.88**	38.25	1.68	**39.93**	0.34	0.34	0	**0.68**
31	1.58	12.34	0	0	**13.92**	0	3.16	**3.16**	7.91	16.14	**24.05**	51.27	0.32	**51.59**	7.28	0	0	**7.28**
32	0	12.04	0	1.96	**14**	0	4.76	**4.76**	20.73	25.77	**46.5**	33.05	0	**33.05**	1.4	0.28	0	**1.68**
33	11.9	13.69	0	0	**25.59**	0	1.49	**1.49**	26.49	12.8	**39.29**	29.76	0.6	**30.36**	3.27	0	0	**3.27**
34	0.89	19.82	0	2.07	**22.78**	0	8.58	**8.58**	6.51	13.61	**20.12**	41.41	5.33	**46.74**	1.78	0	0	**1.78**
35	0	16.47	2.06	2.06	**20.59**	0	0	**0**	17.35	21.18	**38.53**	39.12	1.47	**40.59**	0.29	0	0	**0.29**
36	0	22.86	3.93	2.5	**29.29**	0	0	**0**	26.43	15.36	**41.79**	28.57	0.36	**28.93**	0	0	0	**0**
37	0	22	3.67	1	**26.67**	0	2	**2**	28	11	**39**	31	0.33	**31.33**	1	0	0	**1**
38	0	7.19	0.94	0.63	**8.76**	0	0	**0**	22.5	21.56	**44.06**	46.25	0.63	**46.88**	0	0.31	0	**0.31**
39	1.33	11.67	0	4	**17**	0.33	7.67	**8**	25.33	19	**44.33**	24.67	0	**24.67**	6	0	0	**6**
40	0	2.35	0	0.59	**2.94**	0	0	**0**	23.53	18.82	**42.35**	42.94	11.47	**54.41**	0.29	0	0	**0.29**

Fig. SI 2.1 Variation of benthic cover (%) in each of the 40 transects evaluated at the top of the patches in Recife dos Cascos. MD, *Madracis decactis*; MC, *Montastraea cavernosa*; MHI, *Mussismilia hispida*; SID, *Siderastrea* sp.; TC, *Tubastraea coccinea*; TUB, *Tubastraea* sp.; CAA, Calcareous articulated algae; CCA, Crustose coralline algae; TURF, Turf algae; MAC, Macroalgae; SPO, Sponge; ECH, Echinoderms; SED, Sediment.

Fig. SI 2.2 Biplot representation for Principal Component Analysis (PCA) of the benthic structure of Cascos Reef. The numbers indicate the 40 transects performed at the top of the patches reefs and the red arrows show the benthic groups: MD, *Madracis decactis*; MC, *Montastraea cavernosa*; MHI, *Mussismilia hispida*; SID, *Siderastrea* sp.; TC, *Tubastraea coccinea*; TUB, *Tubastraea* sp.; CAA, Calcareous articulated algae; CCA, Crustose coralline algae; TURF, Turf algae; MAC, Macroalgae; SPO, Sponge; ECH, Echinoderms; SED, Sediment. In the analysis, the Covariance Matrix was used since the raw data were in the same unit.

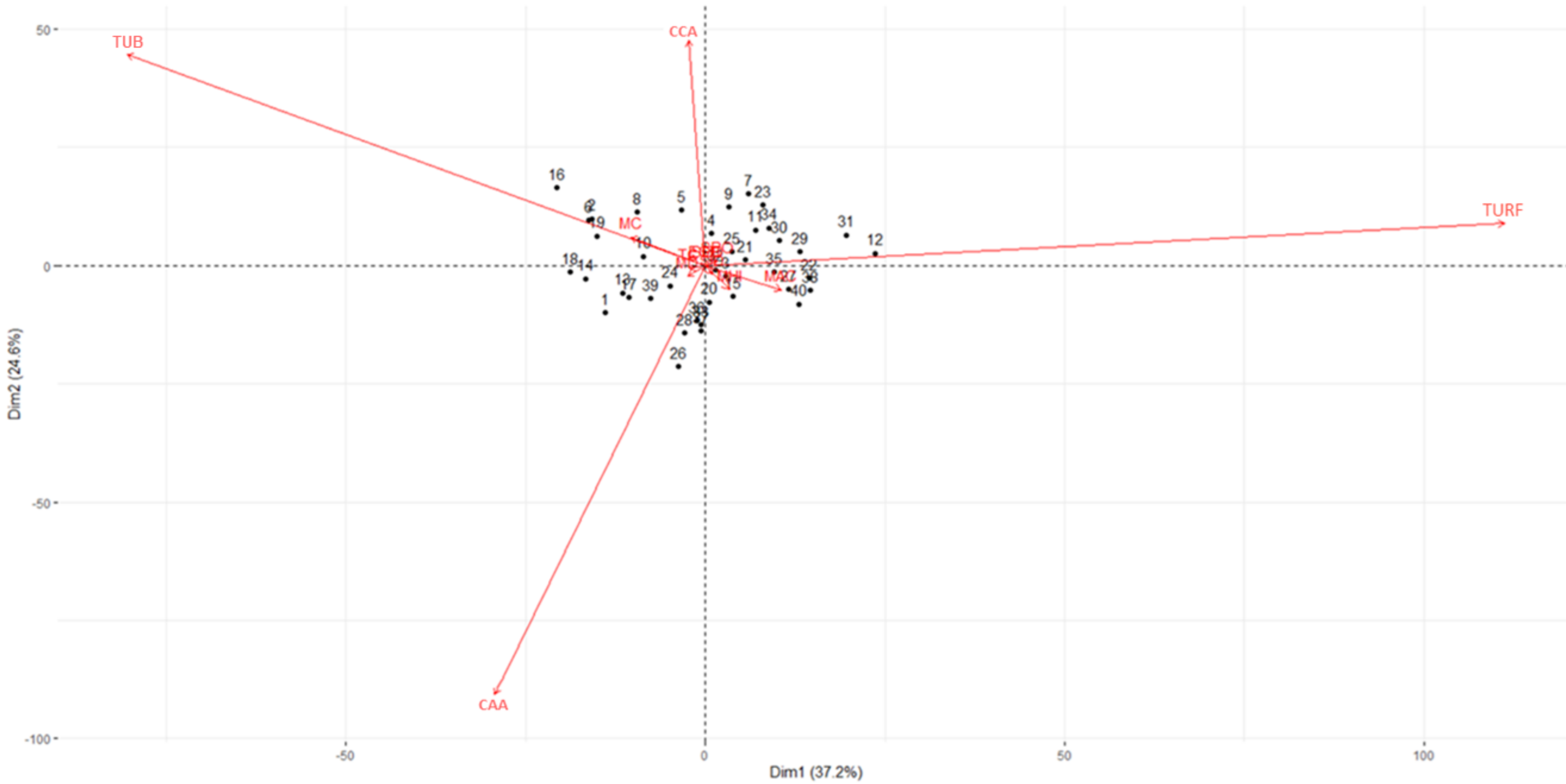

Table SI 2.2 Percentage coverage (%) of native and invasive corals at the top of patches in Cascos Reef considering the 40 transects evaluated. MC, *M. cavernosa*; SID, *Siderastrea* sp.; MD, *M. decactis*; MHI, *M. hispida*; TUB, *Tubastraea* sp.; TC, *T coccinea*. * Average coverage < 1%.

	Native corals				Invasive corals	
	MC	**SID**	**MD**	**MHI***	**TUB**	**TC***
Mean ± SD	11.8 ± 7.4	1.5 ± 1.3	1.1 ± 2.3	0.9 ± 1.5	6.8 ± 8.4	0.1 ± 0.7
Maximum	33.2	5.7	11.9	5.0	29.8	4.7

Supplementary Information 3 To calculate the individual complexity of coral species, we used the ratio between the real surface area and the surface area of the convex contour generated by connecting the most external points of the digital model of the coral colonies digitized and analyzed in the Meshlab software**.** The complexity index of each species (CC_{sp}) was determined from the average of the individual complexities of the colonies collected in Cascos Reef.

Table SI 1 Geometric variables estimated using the Meshlab software. CC_{sp}, Individual complexity index of a given coral species (mean ± standard deviation).

Species/Colony	**Length (cm)**	**Height (cm)**	**Width (cm)**	**Colony area (cm^2)**	**Convex contour area (cm^2)**	**CC_{sp}**
***Tubastraea* sp.**	-	-	-	-	-	**0.77 ± 0.08**
Tub_#1	13.2	7.7	9, 2	607.1	326.6	0.86
Tub_#2	9.1	9.3	8.5	430.3	249.7	0.72
Tub_#3	14.7	9.3	12.5	760.1	443.4	0.71
T. coccinea	-	-	-	-	-	**0.74 ± 0.11**
T_coc_#1	8.4	4.9	7.5	270.5	144.8	0.87
T_coc_#2	7.3	6.0	4.9	201.4	120.3	0.67
T_coc_#3	4.0	3.6	3.8	81.6	48.4	0.68
M. cavernosa	-	-	-	-	-	**0.18 ± 0.01**
M_cav_#1	23.2	14.4	18.0	1213.9	1034.4	0.17
M_cav_#2	15.7	14.0	9.1	650.8	547.0	0.19
***Siderastrea* sp.**	-	-	-	-	-	**0.11 ± 0.02**
Sid_#1	9.0	5.2	8.9	209.6	186.9	0.12
Sid_#2	9.7	4.4	8.0	181.0	165.8	0.09

Supplementary Information 4 Characterization of the reef complexity and the individual contribution of invasive and native species in each of the 40 randomly defined transects under the top of the different patches in Cascos Reef (Bahia, Brazil). Reef rugosity (DRR $_{STD}$) was estimated using a digital probe, as described by Dustan et al. (2013). The individual contribution of invasive corals to the complexity of each evaluated transect (CCI $_{Invader}$) was calculated by the sum of the indices obtained for *Tubastraea* sp. and *T. coccinea*. For native corals, the same attribute was calculated by adding the index obtained for *M. cavernosa* and *Siderastrea* sp. (CCI $_{Native}$).

Table SI 4 Results of the reef complexity and the individual contribution of invasive and native species in the top regions of the Cascos Reef patches. DRR $_{STD}$, Digital Reef Rugosity; CCI$_{sp}$, Contribution Complex Index; MC, *M. cavernosa;* SID*, Siderastrea* sp.; TUB, *Tubastraea* sp.; TC, *T. coccinea.*

Transect	DRR $_{STD}$	CCI$_{sp}$					
		Natives			Invaders		
		MC	SID	CCI $_{Native}$	TUB	TC	CCI $_{Invader}$
1	0.22	0.00	0.53	**0.53**	200.61	0.00	**200.61**
2	0.28	10.53	1.70	**12.24**	251.91	0.00	**251.91**
3	0.62	4.54	4.80	**9.33**	125.57	0.00	**125.57**
4	0.38	2.72	1.70	**4.43**	65.85	0.00	**65.85**
5	0.30	1.27	0.64	**1.91**	180.70	0.00	**180.70**
6	0.61	7.26	0.85	**8.12**	225.11	0.00	**225.11**
7	0.55	3.99	2.45	**6.45**	138.59	0.00	**138.59**
8	0.56	3.63	1.60	**5.23**	266.46	0.00	**266.46**
9	0.87	3.81	0.53	**4.35**	259.57	0.00	**259.57**
10	0.24	9.08	0.32	**9.40**	109.49	0.00	**109.49**
11	0.25	8.17	2.98	**11.15**	5.36	0.00	**5.36**
12	0.59	1.82	1.81	**3.63**	3.83	0.00	**3.83**
13	0.72	4.54	1.39	**5.92**	197.55	0.00	**197.55**
14	0.49	4.36	0.00	**4.36**	336.90	26.72	**363.62**
15	0.54	3.45	0.00	**3.45**	111.02	0.00	**111.02**
16	0.44	3.09	0.00	**3.09**	375.95	0.74	**376.70**
17	0.63	9.62	2.66	**12.29**	68.15	0.00	**68.15**
18	0.69	4.72	1.28	**6.00**	254.21	0.00	**254.21**
19	0.27	7.99	0.75	**8.74**	248.85	0.00	**248.85**
20	0.60	7.26	2.98	**10.25**	61.26	0.00	**61.26**
21	0.46	9.08	1.70	**10.78**	0.00	0.00	**0.00**
22	0.26	5.99	1.17	**7.16**	0.00	0.00	**0.00**
23	0.35	4.54	1.60	**6.14**	0.77	0.00	**0.77**
24	0.82	7.08	2.45	**9.53**	13.78	0.00	**13.78**
25	0.35	8.90	2.02	**10.92**	2.30	0.00	**2.30**
26	0.21	9.62	4.37	**13.99**	0.00	0.00	**0.00**

Transect	DRR_{STD}	CCI$_{sp}$					
		Natives			Invaders		
		MC	SID	**CCI$_{Native}$**	TUB	TC	**CCI$_{Invader}$**
27	0.24	2.72	3.20	**5.92**	17.61	0.00	**17.61**
28	0.25	5.08	1.70	**6.79**	0.77	0.00	**0.77**
29	0.26	3.45	0.11	**3.56**	0.00	0.00	**0.00**
30	0.19	8.72	1.92	**10.63**	0.00	0.00	**0.00**
31	0.50	4.18	0.43	**4.60**	52.83	0.00	**52.83**
32	0.52	5.08	3.62	**8.71**	96.48	0.00	**96.48**
33	0.31	8.17	0.11	**8.28**	26.03	0.00	**26.03**
34	0.54	8.90	2.66	**11.56**	124.04	0.00	**124.04**
35	0.18	9.99	2.77	**12.76**	1.53	0.00	**1.53**
36	0.76	9.08	3.20	**12.28**	1.53	0.00	**1.53**
37	0.24	10.17	1.49	**11.66**	33.69	0.00	**33.69**
38	0.25	5.45	0.64	**6.09**	0.00	0.00	**0.00**
39	0.36	6.36	3.20	**9.55**	94.18	2.23	**96.41**
40	0.19	3.45	1.70	**5.15**	0.00	0.00	**0.00**

References Supplementary Information 4

Dustan P, Doherty O, Pardede S (2013) Digital Reef Rugosity Estimates Coral Reef Habitat Complexity. PLoS ONE 8:e57386

Supplementary Information 5 Characterization of the reef fish assemblage and trophic structure, resulting from visual censuses carried out in each of the 40 randomly defined transects under the top of the different patches in Cascos Reef (Bahia, Brazil). In this study, we used a methodology adapted from Lang et al. (2010). Fish were identified by species and later classified into seven trophic groups based on previous descriptions of trophic categories and feeding behaviors (Floeter et al. 2004; Ferreira et al. 2004; Halpern and Floeter 2008; Longo et al. 2014).

Table SI 5 Results of visual censuses (40 transects) and trophic structure of the fish assemblage in the top regions of the CR patches. TH, Territorial herbivore; PL, Planktivore; RH, Roving Herbivore; O, Omnivore; C, Carnivore; MI, Mobile Invertivore; SI, Sessile Invertivore.

Family	Species (n)	Individuals (N)	Abundance (N m^{-2})	Trophic Groups						
				TH	PL	RH	OM	CA	MI	SI
Acanthuridae	3	50	0.13			50				
Blennidae	1	1	0.00	1						
Carangidae	1	2	0.01					2		
Chaetodontidae	2	24	0.06							24
Cirrhitidae	1	11	0.03						11	
Gobiidae	2	58	0.15				1		57	
Grammatidae	1	5	0.01						5	
Haemulidae	7	2,705	6.76						2,705	
Holocentridae	2	28	0.07		12				16	
Labridae	6	459	1.15		307				152	
Labrisomidae	1	1	0.00						1	
Monacanthidae	2	18	0.05				18			
Mullidae	2	17	0.04						17	
Muraenidae	1	1	0.00					1		
Pempheridae	1	335	0.84		335					
Pomacanthidae	1	22	0.06							22
Pomacentridae	6	2,073	5.18	88	1,949		36			
Scaridae	4	110	0.28			110				
Scorpaenidae	1	2	0.01					2		
Serranidae	6	124	0.31		33			91		
Tetraodontidae	1	3	0.01							3
TOTAL	**52**	**6,049**	**15.12**	**89**	**2,636**	**160**	**55**	**96**	**2,964**	**49**

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Lang JC, Marks KW, Kramer PA, Kramer PR, Ginsburg RN (2010) AGRRA Protocols Version 5.4.

Longo GO, Ferreira CEL, Floeter SR (2014) Herbivory drives large - scale spatial variation in reef fish trophic interactions. Ecol Evol 4:4553–45

Supplementary Information 6 To evaluate the combined effect of structural complexity and benthic cover on the species richness and abundance of fish trophic groups in the Cascos Reef, we used Generalized Linear Models (GLMs). All models designed were submitted to a model selection approach based on the Akaike information criterion corrected for small samples (AICc), where lower values of AIC indicate better model fits.

Table SI 6.1 Selection parameters of the Generalized Linear Models based on the Akaike information criterion (AICc), used to explain the relationship between the dependent variables (fish species richness) and environmental predictors (benthic cover and complexity indices) recorded in 40 random transects in Cascos Reef (Bahia, Brazil). Models ranked by ΔAICc values. Here, we present the most plausible models (i.e., when the difference in AICc between models was less than 2). ΔAICc, difference between AICc compared to the best model; df, number of parameters of the model; wi, weight of the AICc. CCA, Crustose coralline algae; CCI $_{Invader}$, Contribution index of native corals to reef complexity. Highlight in bold for models whose predictor variables were all significant (i.e., P values < 0.05) or when the null model was significant.

Variable	**Model**	**ΔAICc**	**df**	**wi**
Fish species richness	**Null**	**0.0**	**1**	**0.1110**
	CCA	0.9	2	0.0707
	CCI $_{Native}$	1.9	2	0.0430

Table SI 6.2 Selection parameters of the Generalized Linear Models based on the Akaike information criterion (AICc), used to explain the relationship between the dependent variables (abundance of trophic groups of reef fish) and environmental predictors (benthic cover and complexity indices) recorded in 40 random transects in Cascos Reef (Bahia, Brazil). Models ranked by ΔAICc values. Here, we present the most plausible models (i.e., when the difference in AICc between models was less than 2). ΔAICc, difference between AICc compared to the best model; df, number of parameters of the model; wi, weight of the AICc. CAA, Calcareous articulated algae; CCA, Crustose coralline algae; TURF, Turf algae; MAC, Macroalgae; CCI $_{Native}$, Contribution index of native corals to reef complexity; CCI $_{Invader}$, Contribution index of invasive corals to reef complexity; and DRR $_{STD}$, Digital rugosity. Highlight in bold for models whose predictor variables were all significant (i.e., P values < 0.05) or when the null model was significant.

Trophic Group (abundance)	**Model**	**ΔAICc**	**df**	**wi**
Territorial Herbivores (TH)	TURF + MAC	0.0	4	0.0702
	MAC	**0.0**	**3**	**0.0695**
	MAC + CCI $_{Invader}$	0.4	4	0.0588
	TURF + MAC + CCI $_{Native}$	0.4	5	0.0587
	MAC + CCI $_{Native}$	1.1	4	0.0401
	CAA + MAC	1.8	4	0.0285
	CAA + MAC + CCI $_{Invader}$	1.9	5	0.0273

Trophic Group (abundance)	Model	ΔAICc	df	wi
Roving Herbivores (RH)	CAA + CCA + CCI $_{Invader}$	0.0	5	0.1844
	CAA + CCI $_{Invader}$	**0.9**	**4**	**0.1177**
	CAA + MAC + CCI $_{Invader}$	1.4	5	0.0901
	CAA + CCA + MAC + CCI $_{Invader}$	1.8	6	0.0747
Planktivores (PL)	**CAA + CCI $_{Invader}$**	**0.0**	**4**	**0.0402**
	CAA + TURF + DRR $_{STD}$	0.3	5	0.0339
	CCA + TURF	**0.4**	**4**	**0.0336**
	CAA + CCA + CCI $_{Invader}$	0.6	5	0.0302
	CCA + CCI $_{Invader}$	0.6	4	0.0300
	CCA + CCI $_{Invader}$ + DRR $_{STD}$	0.7	5	0.0290
	CCA + DRR $_{STD}$	0.8	4	0.0270
	CAA + MAC + CCI $_{Invader}$	1.3	5	0.0215
	CCA + TURF + MAC	1.3	5	0.0214
	CAA + CCI $_{Invader}$ + DRR $_{STD}$	1.3	5	0.0212
	CCA + MAC + CCI $_{Invader}$	1.7	5	0.0208
	CAA + CCA + CCI $_{Invader}$ + DRR $_{STD}$	1.7	6	0.0176
	CCA + CCI $_{Native}$ + CCI $_{Invader}$	1.7	5	0.0171
	CAA + CCI $_{Native}$ + CCI $_{Invader}$	1.7	5	0.0170
	CCA + TURF + CCI $_{Invader}$	1.8	5	0.0163
Omnivores (OM)	**CCI $_{Invader}$**	**0.0**	**3**	**0.0921**
	CCI $_{Native}$ + CCI $_{Invader}$	0.3	4	0.0809
	CCI $_{Native}$	1.4	3	0.0461
	TURF + CCI $_{Invader}$	1.6	4	0.0416
	CCA + CCI $_{Invader}$	1.6	4	0.0412
Carnivores (CA)	CCI $_{Invader}$	0.0	3	0.0740
	Null	**0.7**	**2**	**0.0514**
	MAC	1.0	3	0.4410
	CCI $_{Native}$ + CCI $_{Invader}$	1.3	4	0.0390
	CCA + CCI $_{Invader}$	1.4	4	0.0366
	MAC + CCI $_{Invader}$	1.5	4	0.0347
Sessile Invertivores (SI)	**TURF**	**0.0**	**3**	**0.1687**
	TURF + MAC	1.7	4	0.0717
Mobile Invertivores (MI)	**Null**	**0.0**	**2**	**0.1021**
	CCA	0.7	3	0.0728
	TURF	1.7	3	0.0436
	DRR $_{STD}$	1.8	3	0.0410

ANEXO A - REGRAS DE FORMATAÇÃO DA REVISTA MARINE ENVIRONMENTAL RESERACH (ARTIGO 1)

Introduction

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- Comments and replies: Comments relate to articles in Marine Biology not older than one year. Their intention has either to be a substantial critique of the original article or the clarification of a major misunderstanding that could have been caused by the original article. The authors of the criticized articles have the right to write a reply. Comment and reply will be published together. The comment will be reviewed externally, while the reply will only be edited for clarity.
- Highlight articles: Outstanding papers of all categories may be selected as highlight articles. These articles must be exceptional in respect to the originality of the study, the importance to a diverse group of marine biologists and to the robustness of the methods. The specific importance of the article is emphasized by an accompanying comment of the responsible Editor. Highlight articles are promoted in social media.

Manuscript Submission

Manuscript Submission

Submission of a manuscript implies: that the work described has not been published before; that it is not under consideration for publication anywhere else; that its publication has been approved by all co-authors, if any, as well as by the responsible authorities – tacitly or explicitly – at the institute where the work has been carried out. The publisher will not be held legally responsible should there be any claims for compensation.

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Authors wishing to include figures, tables, or text passages that have already been published elsewhere are required to obtain permission from the copyright owner(s) for both the print and online format and to include evidence that such permission has been granted when submitting their papers. Any material received without such evidence will be assumed to originate from the authors.

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Please follow the hyperlink “Submit manuscript” and upload all of your manuscript files following the instructions given on the screen.

Source Files

Please ensure you provide all relevant editable source files at every submission and revision. Failing to submit a complete set of editable source files will result in your article not being considered for review. For your manuscript text please always submit in common word processing formats such as .docx or LaTeX.

Title Page

Please make sure your title page contains the following information.

Title

The title should be concise and informative.

Author information

- The name(s) of the author(s)
- The affiliation(s) of the author(s), i.e. institution, (department), city, (state), country
- A clear indication and an active e-mail address of the corresponding author
- If available, the 16-digit ORCID of the author(s)

If address information is provided with the affiliation(s) it will also be published.

For authors that are (temporarily) unaffiliated we will only capture their city and country of residence, not their e-mail address unless specifically requested.

Large Language Models (LLMs), such as ChatGPT, do not currently satisfy our authorship criteria. Notably an attribution of authorship carries with it accountability for the work, which cannot be effectively applied to LLMs. Use of an LLM should be properly documented in the Methods section (and if a Methods section is not available, in a suitable alternative part) of the manuscript.

Abstract

Please provide an abstract of 150 to 250 words. The abstract should not contain any undefined abbreviations or unspecified references.

For *life science journals only (when applicable)*

- Trial registration number and date of registration for prospectively registered trials

- Trial registration number and date of registration, followed by “retrospectively registered” for retrospectively registered trials

Additional Details on General Structure

The manuscript should be submitted as a word file or in LaTeX. The manuscript should be organized into Abstract, Introduction, Materials and Methods, Results, Discussion/Conclusion, Compliance with Ethical Standards, Acknowledgments, References, Figures (with captions) and Tables. Marine Biology does not publish footnotes or supplements, but additional data or videos may be submitted as electronic supplementary material which will be available online.

No full justification for the text should be used. Line numbers should run consecutively throughout the text, from the title page through the figure legends. Lines in tables or figures should not be numbered. Abbreviations and acronyms must be defined at first mention in the Abstract, again in the main body of the text, and also in the Figure Legends. A list of abbreviations may be included as a table, but should not appear at the beginning of the manuscript.

The **Title** should be meaningful and signal the importance of the study for the field. It should be descriptive and tell the reader what the paper is about. It should be general rather than restrictive to species and geographic areas. If scientific names of species are used, they must be accompanied by a higher taxonomic classification term and/or by a common name.

The **Abstract** should summarize the manuscript and attract the reader. It should be short and clear (150-250 words). The abstract should reflect what was done, why it was done, and what major results were obtained. It should not be written in the first person. The abstract should include the date(s) of the study and the latitude and longitude where the samples or experimental organisms were collected. It should not contain descriptions of the state of the art; such information should be limited to the introduction. No undefined abbreviations or unspecified references should be used. The abstract may decide whether a manuscript will be sent out for review; papers may be rejected due to poor or confusing abstracts.

Keywords: The keywords indicated in the submission template should also be included in the manuscript.

The **Introduction** should describe why the study was done and end with some testable hypotheses or clear objectives. Manuscripts which do not present a clear hypothesis are likely to be rejected without review.

Methods: All details required to repeat the work must be provided. Usage of publicly accessible data from repositories must be indicated. The respective accession information must be provided in the References.

Results: Where specific results are being presented or discussed the past tense should be used. The present tense should only be used for generalizations arising from the study results.

The **Discussion** should highlight the importance or significance of the study for the field and the resulting new insights.

Compliance with Ethical Standards must be included as a separate section. The authors should give information about funding and explicitly declare that they have no conflict of interest.

They should also declare that all applicable international, national and/or institutional guidelines for sampling, care and experimental use of organisms for the study have been followed and all necessary approvals have been obtained. Details about permissions should be provided; documentary evidence must be available on request.

Please do not write "Informed consent was obtained from all individual participants included in the study” if (as usual) no human participants were involved in the study.

In the **Acknowledgement** grants, funds, and contributing people should be mentioned. The reviewers should be acknowledged, but please consider that Marine Biology now allows reviewers to have their names disclosed on the manuscript. You might include the name of a reviewer who has agreed to disclose her/his name into the acknowledgements when you receive the proofs (names are printed at the first page of the paper), but this is not mandatory. Write e.g. “We thank the reviewers” or “We thank X.Y. and an anonymous reviewer”

The **References** must be formatted in MABI style (see more details under “Citations”). Data taken/used from public Databases (e.g. PANGAEA) must be cited by accession numbers.

Figures: For ease of reviewing the figures with their captions should be included into the running text. More details are given under ‘Illustrations’ and ‘Figure Captions’ (see below). In addition the figure source files without captions must be submitted.

Tables: Tables should be numbered using Arabic numerals and have a table caption (title) on top, explaining the components of the table. All abbreviations in the table should be explained in the caption. Tables must not contain vertical lines.

Text

Text Formatting

- Manuscripts should be submitted in Word.
- Use a normal, plain font (e.g., 10-point Times Roman) for text.
- Use italics for emphasis.
- Use the automatic page numbering function to number the pages.
- Do not use field functions.
- Use tab stops or other commands for indents, not the space bar.
- Use the table function, not spreadsheets, to make tables.
- Use the equation editor or MathType for equations.
- Save your file in docx format (Word 2007 or higher) or doc format (older Word versions).

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Please use no more than three levels of displayed headings.

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Abbreviations should be defined at first mention and used consistently thereafter.

Footnotes

Footnotes can be used to give additional information, which may include the citation of a reference included in the reference list. They should not consist solely of a reference citation, and they should never include the bibliographic details of a reference. They should also not contain any figures or tables.

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Always use footnotes instead of endnotes.

Acknowledgments

Acknowledgments of people, grants, funds, etc. should be placed in a separate section on the title page. The names of funding organizations should be written in full.

Important note:

Contrary to the above text, the journal does not encourage the use of footnotes.

Additional Details:

- Use 1.5 or double-space formatting and enable line numbering. No full justification for the text should be used. Superscript must be used to denote the denominator in units, e.g. kg y-1, 24 hr time for time of day, e.g. 0700 hr.
- Use of a recent article as a guideline is recommended. Correct formatting is a prerequisite for acceptance of a manuscript. This concerns especially statistics, units, and citations/references.

Scientific style

Genus and species names should be in italics.

Statistics

Describe statistical methods in sufficient detail to allow a knowledgeable reader with access to the original data to verify the reported results. Use the same font for the same mathematical symbol regardless where it appears in the manuscript (text, equations, tables, figures, figure legends).

Give means and standard errors/standard deviations with their associated sample size in the format: X ± SE = 35.09 ± 0.07 km, n = 15. When standard deviation/error is shown in an illustration, n should be given as well.

Statistical tests use the following formats: (ANOVA, F (1,25) = 8.56, P= 0.035)

(Kruskal-Wallis test, H25 = 123.7, P= 0.001) (Chi-square test, X22 = 0.23, P = 0.57) (Paired t test, t24 = 2.33, P= 0.09)

(Linear regression, r2 = 0.94, F1,66 = 306.87, P ‹ 0.001) (Spearman rank correlation, rs = 0.60, N = 33, P ‹ 0.01) (Wilcoxon signed-ranks test, T = 7, N = 33, P ‹ 0.05) (Mann-Whitney U test, U = 44, N1 = 7, N2 = 24, P ‹ 0.02)

Please either give the exact P-value of a statistical test, or state P‹0.0xxx, if this is not possible. P=0 is not valid.

Units

Use of SI and SI-derived units is preferred. Internationally accepted units can be also be used, e.g. “min” for “minute”. The capital letter “L” must be used for liter.

Please use superscripts instead of “/” or “per …” for ratios. Exponents should also be written as superscripts.

When using a number and a unit of measure to make a qualifying adjective, put a hyphen between them, e.g. 300-μm sieve.

Please refer to the following examples.

Length, Area, Volume: pm, nm, μm, mm, cm, m, km, mm2, cm2, m2, L, mL, μL, mm3, cm3, m3 Mass: pg, ng, μg, mg, g, kg, t, Da, kDa

Time: s, min, h, d, y Temperature: °C,

Absolute quantity: pmol, nmol, μmol, mmol, mol

Concentration: pM, nM, μM, mM, M, N, %, μg L-1,

Work, Energy, Heat quantity: J, erg, cal, kcal Force: dyn, N, gw, kgw

Pressure: Pa, mmHg, atm, bar Electricity: V, W, mA, A, Hz

Photometry: if possible, avoid cd, lx, lm, cd m-2, energy or photon flux density would be preferable

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Radioactivity: dpm, cps, cpm, mBq, Bq, kBq, Gy, kGy, mSv, Sv, R, kR Rotation: ×g, cycle Use the symbols ‹ and › to stand for less than and more than.

Also note that salinity has no units and should be presented as: salinity of X or salinity X.

Organisms

Genus and species name must be in italics. It is recommended that the species names appear in full at the beginning of each section of the manuscript and when they appear at the beginning of a sentence. In other places use the contraction e.g. A. islandica for Arctica islandica. Do not abbreviate genus names if several genera with the same initials can lead to confusion, or when only the genus name is used. Genus sp. and Genus spp. should only be used when speciation to species level was generally sought, but not completely reached and several species should be treated together, respectively.

The species author may follow the first use of the study species name in either the Abstract or the Materials and Methods. If it is included, the reference to the original description must appear in the References section.

Common names can be used in addition to the scientific names, they are useful especially in the title. Common names such as “water fleas” for cladocerans, or common names that might be misleading must be avoided. E.g.: Sandfish is a common name of: Gonorynchus, a genus of fish, Scincus scincus, a skink, and Holothuria scabra, a sea cucumber. It should only be used for the fish.

Only use the words ‘animal’ and ‘plant’ in the most general sense. When referring to the individual organisms used in a study, use the most specific term possible such as the species name (in full or contracted), the common name such as ‘mud shrimp’ for Upogebia pugettensis, or ‘individuals’ where appropriate.

When describing the general attributes of a species use a singular verb. When referring to the multiple organisms belonging to the species used in a study, use a plural verb.

Seasons

When describing the seasonal timing of events, be aware that fall and winter occur at different times of the year in the northern and southern hemispheres. It is best to specify the months rather than just the seasons.

Study Locations

When writing the names of states in the USA do not use the postal abbreviation but write them in full− thus Virginia not VA.

If a map is used to show study locations, it must have a scale, an arrow indicating due north or a compass rose and a border with the latitude/longitude marked on it. It should show all geographical locations mentioned in the study. The source of the map must be given in the caption of the figure.

Guidelines for reporting ocean acidification data in scientific journals

A document prepared in the framework of the data management activity of the Ocean Acidification International Coordination Centre of the International Atomic Energy Agency can be found at the following link:

Guidelines for reporting ocean acidification data in scientific journals

References

Citation

Cite references in the text by name and year in parentheses. Some examples:

- Negotiation research spans many disciplines (Thompson 1990).
- This result was later contradicted by Becker and Seligman (1996).
- This effect has been widely studied (Abbott 1991; Barakat et al. 1995a, b; Kelso and Smith 1998; Medvec et al. 1999, 2000).

Reference list

The list of references should only include works that are cited in the text and that have been published or accepted for publication. Personal communications and unpublished works should only be mentioned in the text.

Reference list entries should be alphabetized by the last names of the first author of each work. Please alphabetize according to the following rules: 1) For one author, by name of author, then chronologically; 2) For two authors, by name of author, then name of coauthor, then chronologically; 3) For more than two authors, by name of first author, then chronologically.

If available, please always include DOIs as full DOI links in your reference list (e.g. “https://doi.org/abc”).

- Journal article

  Gamelin FX, Baquet G, Berthoin S, Thevenet D, Nourry C, Nottin S, Bosquet L (2009) Effect of high intensity intermittent training on heart rate variability in prepubescent children. Eur J Appl Physiol 105:731-738. https://doi.org/10.1007/s00421-008-0955-8

  Ideally, the names of all authors should be provided, but the usage of “et al” in long author lists will also be accepted:

  Smith J, Jones M Jr, Houghton L et al (1999) Future of health insurance. N Engl J Med 965:325–329

- Article by DOI

Slifka MK, Whitton JL (2000) Clinical implications of dysregulated cytokine production. J Mol Med. https://doi.org/10.1007/s001090000086

- Book

South J, Blass B (2001) The future of modern genomics. Blackwell, London

- Book chapter

Brown B, Aaron M (2001) The politics of nature. In: Smith J (ed) The rise of modern genomics, 3rd edn. Wiley, New York, pp 230-257

- Online document

Cartwright J (2007) Big stars have weather too. IOP Publishing PhysicsWeb. http://physicsweb.org/articles/news/11/6/16/1. Accessed 26 June 2007

- Dissertation

Trent JW (1975) Experimental acute renal failure. Dissertation, University of California

Always use the standard abbreviation of a journal's name according to the ISSN List of Title Word Abbreviations. If you are unsure, please use the full journal title.

Additional Remarks on Citation

When citing references in the text, put them in parentheses in chronological order with the earliest first. Separate them with semicolons. Do not put a comma between the author(s) and date.

Examples:

- (Thompson 1990; Abbott et al. 2005; Elliott and Green 2009)
- Same author, multiple years. E.g. (Brown 1997, 2000, 2005)
- Same author, same year. E.g. (Brown 2005a, b)
- Two authors (Brown and Smith 2007; Abbott and Green 2009)
- Multiple authors (Zar et al. 1998; Brown et al. 2008)
- As part of a sentence, e.g. This result was later contradicted by Becker and Seligman (1996)
- Abbreviate Personal Communications to (pers comm
- Abbreviate Unpublished data to (unpubl data)

Additional Remarks on References

References should be alphabetized by the last names of the first author of each work.

When there are more than two references with the same first author, the references should be arranged so that the single-authored papers come first in chronological order with the earliest first, then the two-authored papers in alphabetical order by second author, then the multi-authored papers in chronological order with the earliest first.

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Online documents: Websites should only be cited if absolutely essential because they will change with time.

Data from a database must be cited in the references by using a Digital Object Identifier (DOI).

Conference Proceedings should not be cited. Every cited printed work should be publicly accessible by ISBN or ISSN number.

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The results of the reference checking are provided by clicking the corresponding link provided in your "Main Menu" in the Editorial Manager, as well as in the PDF file containing your manuscript. If "not validated" is displayed for a reference, it should be checked carefully and corrected where appropriate, as in most cases typos, wrong journals, issues or pages preclude its validation.

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The following statements must be included in your submitted manuscript under the heading 'Statements and Declarations'. This should be placed after the References section. Please note that submissions that do not include required statements will be returned as incomplete.

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Please describe any sources of funding that have supported the work. The statement should include details of any grants received (please give the name of the funding agency and grant number).

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"*The authors declare that no funds, grants, or other support were received during the preparation of this manuscript.*"

Competing Interests

Authors are required to disclose financial or non-financial interests that are directly or indirectly related to the work submitted for publication. Interests within the last 3 years of beginning the work (conducting the research and preparing the work for submission) should be reported. Interests outside the 3-year time frame must be disclosed if they could reasonably be perceived as influencing the submitted work.

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Please refer to the "Authorship Principles" section below for more information on how to complete this section.

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All original research must include a Data Availability Statement. Data Availability Statements should provide information on where data supporting the results reported in the article can be found. Statements should include, where applicable, hyperlinks to publicly archived datasets analysed or generated during the study. When it is not possible to share research data publicly, for instance when individual privacy could be compromised, data availability should still be stated in the manuscript along with any conditions for access.

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"*The datasets generated during and/or analysed during the current study are available in the [NAME] repository, [PERSISTENT LINK TO DATASETS]*"

"*The datasets generated during and/or analysed during the current study are not publicly available due to [REASON(S) WHY DATA ARE NOT PUBLIC] but are available from the corresponding author on reasonable request.].*"

Please refer to the "Research Data Policy and Data Availability" section below for more information on how to complete this section.

In addition to the above, manuscripts that report the results of studies involving humans and/or animals should include the following declarations:

Ethics approval

Authors of research involving human or animal subjects should include a statement that confirms that the study was approved (or granted exemption) by the appropriate institutional and/or national research ethics committee (including the name of the ethics committee and reference number, if available). For research involving animals, their data or biological material, authors should supply detailed information on the ethical treatment of their animals in their submission. If a study was granted exemption or did not require ethics approval, this should also be detailed in the manuscript.

"*This study was performed in line with the principles of the Declaration of Helsinki. Approval was granted by the Ethics Committee of University B (Date.../No....).*"

"*This is an observational study. The XYZ Research Ethics Committee has confirmed that no ethical approval is required.*"

For detailed information on relevant ethical standards and criteria, please refer to the sections on "Research involving human participants, their data or biological material", "Research involving animals, their data or biological material".

Consent to participate

For all research involving human subjects, freely-given, informed consent to participate in the study must be obtained from participants (or their parent or legal guardian in the case of children under 16) and a statement to this effect should appear in the manuscript.

Example statement:

"*Informed consent was obtained from all individual participants included in the study.*"

"*Written informed consent was obtained from the parents.*"

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Individuals may consent to participate in a study, but object to having their data published in a journal article. If your manuscript contains any individual person's data in any form (including any individual details, images or videos), consent for publication must be obtained from that person, or in the case of children, their parent or legal guardian. This is in particular applicable to case studies. A statement confirming that consent to publish has been received from all participants should appear in the manuscript.

Example statement:

"*The authors affirm that human research participants provided informed consent for publication of the images in Figure(s) 1a, 1b and 1c.*"

Please refer to the section on "Informed Consent" for additional help with completing this information.

Tables

- All tables are to be numbered using Arabic numerals.
- Tables should always be cited in text in consecutive numerical order.

- For each table, please supply a table caption (title) explaining the components of the table.
- Identify any previously published material by giving the original source in the form of a reference at the end of the table caption.
- Footnotes to tables should be indicated by superscript lower-case letters (or asterisks for significance values and other statistical data) and included beneath the table body.

Artwork and Illustrations Guidelines

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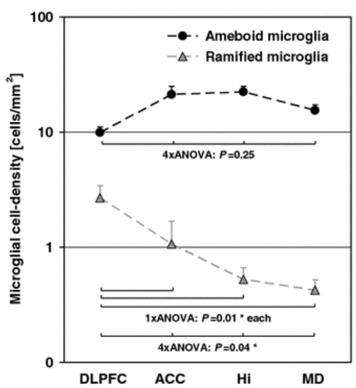
- Supply all figures electronically.
- Indicate what graphics program was used to create the artwork.
- For vector graphics, the preferred format is EPS; for halftones, please use TIFF format. MS Office files are also acceptable.
- Vector graphics containing fonts must have the fonts embedded in the files.
- Name your figure files with "Fig" and the figure number, e.g., Fig1.eps.

Line Art



- Definition: Black and white graphic with no shading.
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- All lines should be at least 0.1 mm (0.3 pt) wide.
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- Vector graphics containing fonts must have the fonts embedded in the files.

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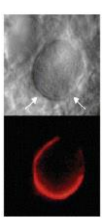

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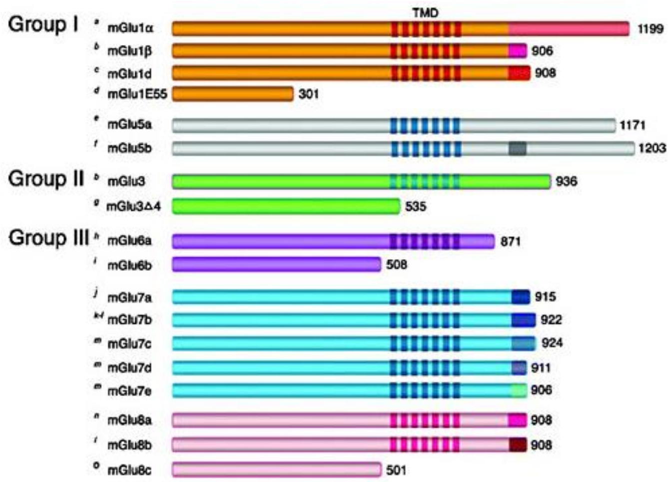

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- Color illustrations should be submitted as RGB.

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- Figures should always be cited in text in consecutive numerical order.
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- If an appendix appears in your article and it contains one or more figures, continue the consecutive numbering of the main text. Do not number the appendix figures, "A1, A2, A3, etc." Figures in online appendices [Supplementary Information (SI)] should, however, be numbered separately.

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- Each figure should have a concise caption describing accurately what the figure depicts. Include the captions in the text file of the manuscript, not in the figure file.
- Figure captions begin with the term Fig. in bold type, followed by the figure number, also in bold type.
- No punctuation is to be included after the number, nor is any punctuation to be placed at the end of the caption.
- Identify all elements found in the figure in the figure caption; and use boxes, circles, etc., as coordinate points in graphs.

- Identify previously published material by giving the original source in the form of a reference citation at the end of the figure caption.

Figure Placement and Size

- Figures should be submitted within the body of the text. Only if the file size of the manuscript causes problems in uploading it, the large figures should be submitted separately from the text.
- When preparing your figures, size figures to fit in the column width.
- For large-sized journals the figures should be 84 mm (for double-column text areas), or 174 mm (for single-column text areas) wide and not higher than 234 mm.
- For small-sized journals, the figures should be 119 mm wide and not higher than 195 mm.

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In order to give people of all abilities and disabilities access to the content of your figures, please make sure that

- All figures have descriptive captions (blind users could then use a text-to-speech software or a text-to-Braille hardware)
- Patterns are used instead of or in addition to colors for conveying information (color-blind users would then be able to distinguish the visual elements)
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Important note:

- In addition to the submission of the figure source files without captions (as mentioned above), the figures with their captions should also be included into the running text.

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The illustrations are a very important part of the article. They must be prepared very carefully and be of good quality. Note that EXCEL is not a drawing program and figures generated in this program frequently require editing prior to inclusion in manuscripts. Legend material should be included on the panels, not hanging off to the side or as titles or labels at the top or bottom of the figures. Legend material can also be included in the figure legend if it does not fit on the panel(s). Manuscripts containing poor quality figures will not be considered for publication. The figures should be as simple as possible and all details must be clearly visible when the figures are reduced in size. Data should be provided in figures OR in tables. Data must not appear twice (Fig and Table).

Any information that is not absolutely necessary for understanding the article should be provided as numbered appendices in the electronic supplementary material (ESM).

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To avoid confusion, no extra list of figure captions should be submitted.

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Observational studies (STROBE)

Systematic reviews and meta-analyses (PRISMA) and protocols (Prisma-P)

Diagnostic/prognostic studies (STARD) and (TRIPOD)

Case reports (CARE)

Clinical practice guidelines (AGREE) and (RIGHT)

Qualitative research (SRQR) and (COREQ)

Animal pre-clinical studies (ARRIVE)

Quality improvement studies (SQUIRE)

Economic evaluations (CHEERS)

Summary of requirements

The above should be summarized in a statement and placed in a 'Declarations' section before the reference list under a heading of 'Ethics approval'.

Please see the various examples of wording below and revise/customize the sample statements according to your own needs.

Examples of statements to be used when ethics approval has been obtained:

- All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki Declaration and its later amendments or comparable ethical standards. The study was approved by the Bioethics Committee of the Medical University of A (No. ...).
- This study was performed in line with the principles of the Declaration of Helsinki. Approval was granted by the Ethics Committee of University B (Date.../No. ...).

- Approval was obtained from the ethics committee of University C. The procedures used in this study adhere to the tenets of the Declaration of Helsinki.
- The questionnaire and methodology for this study was approved by the Human Research Ethics committee of the University of D (Ethics approval number: ...).

Examples of statements to be used for a retrospective study:

- Ethical approval was waived by the local Ethics Committee of University A in view of the retrospective nature of the study and all the procedures being performed were part of the routine care.
- This research study was conducted retrospectively from data obtained for clinical purposes. We consulted extensively with the IRB of XYZ who determined that our study did not need ethical approval. An IRB official waiver of ethical approval was granted from the IRB of XYZ.
- This retrospective chart review study involving human participants was in accordance with the ethical standards of the institutional and national research committee and with the 1964 Helsinki Declaration and its later amendments or comparable ethical standards. The Human Investigation Committee (IRB) of University B approved this study.

Examples of statements to be used when no ethical approval is required/exemption granted:

- This is an observational study. The XYZ Research Ethics Committee has confirmed that no ethical approval is required.
- The data reproduced from Article X utilized human tissue that was procured via our Biobank AB, which provides de-identified samples. This study was reviewed and deemed exempt by our XYZ Institutional Review Board. The BioBank protocols are in accordance with the ethical standards of our institution and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

Authors are responsible for correctness of the statements provided in the manuscript. See also Authorship Principles. The Editor-in-Chief reserves the right to reject submissions that do not meet the guidelines described in this section.

Research involving animals, their data or biological material

The welfare of animals (vertebrate and higher invertebrate) used for research, education and testing must be respected. Authors should supply detailed information on the ethical treatment of their animals in their submission. For that purpose they may use the ARRIVE checklist which is designed to be used when submitting manuscripts describing animal research.

For studies involving client-owned animals, authors must also document informed consent from the client or owner and adherence to a high standard (best practice) of veterinary care.

Authors are recommended to comply with:

- The International Union for Conservation of Nature (IUCN) Policy Statement on Research Involving Species at Risk of Extinction and consult the IUCN red list index of threatened species.
- Convention on the Trade in Endangered Species of Wild Fauna and Flora

When reporting results authors should indicate:

- … that the studies have been approved by a research ethics committee at the institution or practice at which the studies were conducted. Please provide the name of ethics committee and relevant permit number;
- … whether the legal requirements or guidelines in the country and/or state or province for the care and use of animals have been followed.

Researchers from countries without any legal requirements or guidelines voluntarily should refer to the following sites for guidance:

- The Basel Declaration describes fundamental principles of using animals in biomedical research
- The International Council for Laboratory Animal Science (ICLAS) provides ethical guidelines for researchers as well as editors and reviewers
- The Association for the study of Animal Behaviour describes ethical guidelines for the treatment of animals in research and teaching
- The International Association of Veterinary Editors' Consensus Author Guidelines on Animal Ethics provide guidelines for authors on animal ethics and welfare

Researchers may wish to consult the most recent (ethical) guidelines available from relevant taxon-oriented professional societies.

If a study was granted exemption or did not require ethics approval, this should also be detailed in the manuscript.

Summary of requirements

The above should be summarized in a statement and placed in a 'Declarations' section before the reference list under a heading of 'Ethics approval'.

Please see the various examples of wording below and revise/customize the sample statements according to your own needs.

Examples of statements to be used when ethics approval has been obtained:

- All procedures involving animals were in compliance with the European Community Council Directive of 24 November 1986, and ethical approval was granted by the Kocaeli University Ethics Committee (No. 29 12 2014, Kocaeli, Turkey).
- All procedures performed in the study were in accordance with the ARVO Statement for Use of Animals in Ophthalmic Vision and Research. The ethical principles established by the National Institutes of Health Guide for the Care and Use of Laboratory Animals (NIH Publications No. 8523, revised 2011) were followed. The research protocol was approved by the Ethics Committee on Animal Use (Protocol No. 06174/14) of FCAV/Unesp, Jaboticabal.
- This study involved a questionnaire-based survey of farmers as well as blood sampling from their animals. The study protocol was assessed and approved by Haramaya University, research and extension office. Participants provided their verbal informed consent for animal blood sampling as well as for the related survey questions. Collection of blood samples was carried out by veterinarians adhering to the regulations and guidelines on animal husbandry and welfare.
- All brown bear captures and handling were approved by the Ethical Committee on Animal Experiments, Uppsala, Sweden (Application C18/15) and the Swedish Environmental Protection Agency in compliance with Swedish laws and regulations.
- The ethics governing the use and conduct of experiments on animals were strictly observed, and the experimental protocol was approved by the University of Maiduguri Senate committee on Medical Research ethics. Proper permit and consent were obtained from the Maiduguri abattoir management, before the faecal samples of the cattle and camels slaughtered in this abattoir were used for this experiment.

Examples of statements to be used when no ethical approval is required/exemption granted:

- No approval of research ethics committees was required to accomplish the goals of this study because experimental work was conducted with an unregulated invertebrate species.
- As the trappings of small mammals were conducted as part of regular pest control measures in accordance with the NATO Standardized Agreement 2048 "Deployment Pest and Vector Surveillance and Control ", no approval by an ethics committee was required.

- All experiments have been conducted as per the guidelines of the Institutional Animal Ethics Committee, Department of Zoology, Utkal University, Bhubaneswar, Odisha, India. However, the insect species used in this study is reared for commercial production of raw silk materials, as a part of agro-based industry. Therefore, use of this animal in research does not require ethical clearance. We have obtained permission from the office of Research officer sericulture, Baripada, Orissa, India for the provision of infrastructure and support for rearing of silkworm both in indoor and outdoor conditions related to our study to promote sericulture practices.

Authors are responsible for correctness of the statements provided in the manuscript. See also Authorship Principles. The Editor-in-Chief reserves the right to reject submissions that do not meet the guidelines described in this section.

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ANEXO C – COMPROVANTE DE SUBMISSÃO DO ARTIGO 1

Lucas Neves da Rocha

Marine Environmental Research

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Submissions Being Processed for Author

Page: 1 of 1 (1 total submissions)

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Action	Manuscript Number	Title	Initial Date Submitted	Status Date	Current Status
Action Links	MERE-D-24-01567	Growth patterns of invasive sun corals can modulate the bioconstruction potential of coral reefs	Nov 11, 2024	Nov 11, 2024	With Editor

12/11/2024, 00:01 Gmail - Confirming handling editor for submission to Marine Environmental Research

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ANEXO D – COMPROVANTE DE PUBLICAÇÃO DO ARTIGO 2

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Action	Manuscript Number	Title	Initial Date Submitted	Status Date	Current Status	Date Final Disposition Set	Final Disposition
View Submission View Decision Letter View Attachments	MABI-D-23-00225	Effects of invasive sun corals on habitat structural complexity mediate reef trophic pathways	14 Jun 2023	11 Jan 2024	Completed	11 Jan 2024	Accept

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Marine Biology (2024) 171:76
https://doi.org/10.1007/s00227-024-04394-6

ORIGINAL PAPER

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Effects of invasive sun corals on habitat structural complexity mediate reef trophic pathways

Lucas S. Neves da Rocha[1] · José Anchieta C. C. Nunes[2] · Ricardo J. Miranda[3] · Ruy K. P. Kikuchi[1]

Received: 14 June 2023 / Accepted: 10 January 2024

Abstract
Biological invasions have modified habitat structure, forcing changes in ecosystem functions. Structural complexity modulates diversity and trophic pathways, but the roles of invasive species in mediating coral reef habitat attributes and trophic effects are poorly understood. We investigated the influence of invasive corals on reef structural complexity and their implications on reef fish trophic structure. To assess habitat complexity and trophic relationships, we used a digital probe to map reef rugosity and characterized benthic cover and fish abundances by video and visual estimates. We calculated a coral skeleton complexity index (for individual invasive and native colonies) by building high-resolution three-dimensional models with photogrammetry techniques. The study was conducted between February 2018 and March 2019 in Cascos Reef, located on the east coast of Brazil. We reveal that the complex morphology of the invasive coral *Tubastraea* spp. skeleton had a significant positive effect on reef rugosity, contributing to substrate complexity at a sub-metric scale. However, this likely did not promote reef fish diversity but altered the assemblage structure patterns, demonstrated by a negative relationship between coral colony complexity index and abundance of trophic groups such as roving herbivores and omnivores and a positive relationship with planktivores. Thus, our findings support that habitat attribute modification promoted by invasive corals can influence the benthos-fish dynamic, promoting some fish groups to the detriment of others, with pervasive implications for ecosystem functions. Global changes are increasing invasions worldwide, enhancing the need for effective policies for regulation and management to ensure human well-being and ecosystem services.

Keywords Habitat modification · Biological invasions · *Tubastraea* spp. · Reef fish