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Criptofauna associada a banco de rodolitos - o efeito da morfologia versus a
profundidade

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André Florencio Bogo Macedo

Criptofauna de duas espécies de rodolitos antes e após a passagem de uma onda calor em um banco do Atlântico Sul

O presente trabalho em nível de Mestrado foi avaliado e aprovado, 24 de Agosto de 2023, pela banca examinadora composta pelos seguintes membros:

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

Coordenação do Programa de Pós-Graduação

Prof. Dr. Paulo Antunes Horta Junior
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RESUMO

Leitos de rodolitos são habitats bentônicos ecologicamente importantes formados por algas vermelhas calcárias, amplamente distribuídos latitudinalmente e variadas profundidades. Fornecem serviços ecossistêmicos importantes, incluindo o potencial de mitigação das mudanças climáticas e suporte à biodiversidade. Apesar disso, esses ambientes ainda permanecem pouco estudados. Os rodolitos influenciam a diversidade e abundância da criptofauna associada por meio de sua complexidade estrutural e oferta de micro-habitats. Neste estudo, examinamos a comunidade de criptofauna associada a duas espécies formadoras de rodolitos, *Lithophyllum atlanticum* e *Melyvonnea erubescens*, com formas de crescimento distintas, em um banco de rodolitos localizado na Reserva Biológica Marinha do Arvoredo, no Atlântico Sudoeste. Avaliamos os efeitos da complexidade estrutural dos rodolitos, profundidade e estações do ano na composição da comunidade de criptofauna associada. Nossos resultados revelaram diferenças significativas na composição da comunidade de criptofauna entre as duas espécies em diferentes profundidades. Características estruturais, como volume e densidade de ramos, variaram entre as espécies e influenciaram sua fauna associada. A profundidade e a estação do ano parecem impactar indiretamente a distribuição da comunidade, e a densidade de ramos parece ser o fator mais relevante que influencia as diferenças nas comunidades de criptofauna. Nossos resultados enfatizam a importância ecológica dos leitos de rodolitos e destacam a necessidade de pesquisas adicionais para melhor compreender sua conservação e significado ecológico. Proteger essas áreas sensíveis de potenciais impactos é imperativo para preservar a biodiversidade e os serviços ecossistêmicos, considerando que a unidade de conservação discutida aqui enfrenta tentativas de ser transformada em uma área mais permissiva.

Palavras-chave: Macrofauna; Algas calcárias; Ecologia marinha; Biodiversidade; Atlântico Sudoeste

ABSTRACT

Rhodolith beds are ecologically important benthic habitats formed by coralline red algae, found across a wide range of latitudes and depths. They provide crucial ecosystem services, including climate change mitigation and biodiversity support, yet remain understudied. Rhodoliths are known to influence the diversity and abundance of associated cryptofauna through their structural complexity and microhabitat provision. In this study, we examined the cryptofaunal community associated with two rhodolith-forming species, *Lithophyllum atlanticum* and *Melyvonnea erubescens*, with distinct growth forms, in a rhodolith bed located at a no-take area in the SW Atlantic. We evaluated the effects of rhodolith structural complexity, depth and seasons on cryptofaunal community composition. Our findings revealed significant differences in cryptofaunal community composition between the two species at different depths. Structural characteristics, such as volume and branch density, varied between species and influenced their associated fauna. Depth and season seem to indirectly impact community distribution, as well branch density appears to be the most relevant driver influencing cryptofaunal assemblages differences. Our findings emphasize the ecological importance of rhodolith beds and highlights the need for further research to better understand their conservation and ecological significance. Protecting sensitive rhodolith beds from potential impacts is crucial for preserving biodiversity and ecosystem services, as the *no-take* area in discussion here faces an attempt to be transformed into a more permissive area.

Keywords: Macrofauna; Coralline red algae; Marine Ecology; Biodiversity; SW Atlantic

1. INTRODUÇÃO GERAL

Os rodolitos são algas vermelhas calcárias, formando nódulos de vida livre, mais ou menos ramificados, e sistematicamente não geniculadas.(Foster, 2001). Eles são formados pelo crescimento destas algas ao redor de fragmentos de algas calcárias, de corais, conchas ou rochas, sujeitos à movimentação de ondas, correntes ou bioturbação (Marrack, 1999; Foster et al., 2013). À medida que os rodolitos giram, camadas de algas calcárias se acumulam sequencialmente ao redor desses núcleos (Bosence, 1983). Os rodolitos geralmente crescem entre 0.5 e 1.5 mm por ano, com um máximo relatado de 2.7 mm por ano (Frantz et al., 2000; Blake e Maggs, 2003; Amado-Filho et al., 2012; Darrenougue et al., 2013). Seu crescimento pode continuar por décadas ou séculos, à medida que rolam sobre o substrato bentônico (Foster, 2002; McConnico et al. 2014). Possuem uma ampla distribuição global, desde os trópicos até as regiões polares, e são encontrados em uma grande faixa de profundidade, chegando até 268 metros (Bosence, 1983; Littler et al., 1986; McCoy & Kamenos, 2015; Riosmena-Rodríguez et al., 2017).

Bancos de rodolitos são ecossistemas bentônicos estruturalmente complexos, e para além da importância ecológica, incluindo o potencial de mitigação das mudanças climáticas e o provisionamento de biodiversidade, a pesquisa acerca dos bancos de rodolitos ainda são pouco numerosas e recebem relativamente pouco apoio financeiro por parte de governos e iniciativa privada (Tuya et al., 2023).

A morfologia e complexidade interna dos rodolitos suporta uma diversificada criptofauna (termo aplicado aos animais que vivem dentro e sobre os rodolitos) de invertebrados (Nelson, 2009), com padrões de crescimento e bioerosão contribuindo para espaços vazios internos frequentemente intrincados (Basso, 2009; Nebelsick et al., 2011; Nitsch et al., 2015). O relevo heterogêneo e espaços intra-talo fornecem abrigo contra abrasão e predação (Spieler et al., 2001), atraem detritívoros acumulando detritos (Keegan, 1974) e sustentam o assentamento de larvas (Steller et al., 2003; Steller e Cáceres-Martínez, 2009). Por isso, os rodolitos são considerados engenheiros de ecossistemas autogênicos, pois sua complexidade morfológica tende a aumentar a heterogeneidade do ambiente em que estão inseridos, favorecendo a sobrevivência e o assentamento de diferentes organismos (Jones, Lawton e Shachak, 1994). Os espaços intersticiais dentro dos esqueletos dos rodolitos são importantes

micro-habitats para uma diversificada fauna e flora, podendo abrigar esporos e propágulos de macro e microalgas em sua porção endolítica, atuando como "bancos de sementes" e sendo considerados pontos de elevada biodiversidade (Amado-Filho, 2010; Peña et al., 2014; Ordines et al., 2015; Lundquist et al., 2017; Krayesky-Self et al., 2017; Fredericq et al., 2019; Veras et al., 2020), substancialmente maior do que bancos de areias adjacentes (Nelson, 2009). Pesquisadores têm encontrado novos organismos crípticos com frequência (Clark, 2000), enfatizando a importância do estudo das comunidades criptofaunais associadas aos rodolitos.

Esses habitats criados pelos rodolitos também representam importantes áreas de berçário, servem como refúgio contra a predação e representam um habitat de peixes recifais importante e subestimado (Jackson et al., 2004; Kamenos, Moore & Hall-Spencer, 2004; Meihoub Berlandi et al., 2012; Teichert, 2014; Prata et al., 2017; Moura et al., 2021). Além de suas funções ecológicas importantes, os bancos de rodolitos também são fundamentais sumidouros de carbono e devem desempenhar um papel significativo nas discussões sobre o crédito de de carbono (Amado-Filho et al., 2012; van der Heijden & Kamenos, 2015). Conseqüentemente, a presença de bancos de rodolitos aumenta a biodiversidade local, proporcionando e sustentando múltiplos serviços ecossistêmicos (Foster, 2001; Steller et al., 2003).

Embora pareça claro a importância da estrutura tridimensional na condução dos padrões das espécies associadas, há apenas alguns estudos visando o estabelecimento da comunidade criptofaunal em rodolitos, levando inconclusões sobre quais fatores são mais importantes para esses padrões (Steller e Cáceres-Martínez, 2009). Com relação à complexidade estrutural dos nódulos, De Grave, 1999, formulou a hipótese de que a forma do espaço intersticial sustenta a assembléia de crustáceos associados e atesta a importância da estrutura tridimensional dos rodolitos. Otero-Ferrer et al., 2019 concluíram que a colonização faunística inicial é mais influenciada pela heterogeneidade dos nódulos (definida por concavidade, convexidade, epibiontes por exemplo) do que pelo tamanho dos rodolitos experimentais. Concordando com isso, Steller et al., 2003, descobriram que a complexidade do talo é um fator importante para o estabelecimento de uma comunidade associada, embora o espaço disponível (volume do talo) também pareça ter grande importância. A disponibilidade de espaço, refúgio e recursos, fornecida pela complexidade dos talos, parece ser um bom preditor para a abundância e riqueza de

espécies, o que apoia a hipótese de que um aumento na complexidade estrutural conduz à diversidade de espécies (Weber-Van Bosse e Foslie, 1904).

Porém, variações de fatores ambientais, também podem influenciar a estrutura e morfologia dos rodolitos (Bosence, 1976; Steller and Foster, 1996), o que leva a alterações na estrutura da comunidade associada. A sazonalidade pode influenciar a distribuição da comunidade criptofaunal em rodolitos (Foster et al., 2007; Riosmena-Rodríguez e Medina-López, 2010; Otero-Ferrer et al., 2020), assim como a profundidade também pode ser um fator importante, uma vez que modula diretamente as taxas de crescimento (Bahia et al., 2010). Recentemente, Veras et al., 2020, descobriram que as zonas eufóticas podem abrigar o dobro da abundância de organismos e número de táxons em comparação com a zona mesofótica. Além disso, verificou-se que a porosidade aumenta a biodiversidade em um ambiente ártico (Teichert, 2014). Por sua vez, a presença de bioengenheiros, como o peixe *Malacanthus plumieri* (Pereira-Filho et al., 2015), e a idade dos rodolitos (McConnico et al., 2014) podem afetar indiretamente a estrutura de um leito de rodolitos ou individualmente. Há vários fatores que potencialmente, direta ou indiretamente, afetam a estrutura de comunidades associadas aos rodolitos.

Os bancos de rodolitos são vulneráveis a diversas atividades antropogênicas, como sedimentação, mudanças climáticas, dragagem e ancoragem, que podem afetar sua complexidade estrutural. Apesar da importância ecológica desses ambientes bentônicos, a criptofauna associada aos rodolitos ainda é pouco explorada, e não há consenso sobre os principais fatores que influenciam sua diversidade e abundância (Steller & Cáceres-Martínez, 2009), pois diferentes estudos têm encontrado respostas variadas e discordantes. Algumas pesquisas indicam que a morfologia dos rodolitos, como volume/tamanho e/ou o tamanho dos “ramos” podem influenciar a composição da comunidade de criptofauna (Steller et al., 2003; Meihoub Berlandi et al., 2012; Mendéz Trejo et al., 2020), enquanto outras não relataram diferenças para espécies de formas de crescimento distintas (Hinojosa-Arango & Riosmena-Rodríguez, 2004; Harvey & Bird, 2008). Além disso, alguns estudos concluíram que a estrutura tridimensional dos rodolitos é um fator-chave que influencia a fauna associada (Steller et al., 2003; Otero-Ferrer et al., 2019). Características ambientais físicas também podem influenciar indiretamente a composição criptofaunal dos rodolitos (Abrecht et al., 2021).

A falta de compreensão sobre quais aspectos da estrutura tridimensional dos rodolitos (como volume, tamanho, diâmetro, esfericidade, tamanho dos “ramos” e espaço livre interno) são o principal fator de complexidade em um nódulo de rodolito é um desafio atual, uma vez que a tentativa de quantificar essas características é recente (Jardim et al., 2022). Ainda não se sabe se essa complexidade estrutural é o fator mais importante que influencia as comunidades associadas de criptofauna ou se as interações específicas entre espécies são mais significativas, uma vez que interações químicas entre as espécies formadoras de rodolitos e a fauna associada podem afetar a estrutura da comunidade (Steller & Cáceres-Martínez, 2009).

Considerando esse cenário, nosso objetivo foi avaliar a criptofauna associada a duas espécies formadoras de rodolitos, *Lithophyllum atlanticum* (Vieira-Pinto, M.C Oliveira & P.A Horta 2008) e *Melyvonnea erubescens* ((Foslie) Athanasiadis & D.L Ballantine 2014). Ambas as espécies ocorrem concomitantemente em um banco de rodolitos no Atlântico Sudoeste e apresentam formas de crescimento diferentes. Seguindo a terminologia padronizada elaborada por Woerkeing et al., 1993. *M. erubescens* apresenta uma morfologia “fruticosa a verrugosa”, altamente ramificada e com protuberâncias mais curtas (1,5 - 4 mm de comprimento, 1-2 mm de diâmetro) (Sissini et al., 2014), enquanto *L. atlanticum* apresenta uma superfície “lisa ou verrugosa” com protuberâncias maiores (5-10 mm de comprimento, 3,5 mm de diâmetro) (Vieira-Pinto et al., 2014).

Aqui descrevemos a estrutura da comunidade de macroinvertebrados criptofaunal associada a duas espécies formadoras de rodolitos, com diferentes formas de crescimento, e testamos se (1) complexidade estrutural; (2) profundidade e (3) diferentes momentos do ano afetam a estrutura dessa assembleia associada.

ARTIGO

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Cryptofaunal diversity in a SW Atlantic rhodolith bed - morphology effect versus depth

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Abstract

Rhodolith beds are ecologically important benthic habitats formed by coralline red algae, found across a wide range of latitudes and depths. They provide crucial ecosystem services, including climate change mitigation and biodiversity support, yet remain understudied. Rhodoliths are known to influence the diversity and abundance of associated cryptofauna through their structural complexity and microhabitat provision. In this study, we examined the cryptofaunal community associated with two rhodolith-forming species, *Lithophyllum atlanticum* and *Melyvonnea erubescens*, with distinct growth forms, in a rhodolith bed located at a no-take area in the SW Atlantic. We evaluated the effects of rhodolith structural complexity, depth and seasons on cryptofaunal community composition. Our findings revealed significant differences in cryptofaunal community composition between the two species at different depths. Structural characteristics, such as volume and branch density, varied between species and influenced their associated fauna. Depth and season seem to indirectly impact community distribution, as well as branch density appears to be the most relevant driver

influencing cryptofaunal assemblages differences. Our findings emphasize the ecological importance of rhodolith beds and highlights the need for further research to better understand their conservation and ecological significance. Protecting sensitive rhodolith beds from potential impacts is crucial for preserving biodiversity and ecosystem services, as the *no-take* area in discussion here faces an attempt to be transformed into a more permissive area.

Keywords

Macrofauna; Coralline red algae; Marine Ecology; Biodiversity; SW Atlantic

1. INTRO

Rhodolith beds are structurally complex benthic habitats formed by free-living coralline red algae, found in a wide latitudinal (from the tropics to polar regions) and depth range (down to 268 metres) (Bosence, 1983; Littler et al., 1986; Foster, 2001; McCoy & Kamenos, 2015; Riosmena-Rodríguez et al., 2017). Despite great ecological importance, including potential climate change mitigation and provisioning biodiversity, rhodolith beds remain unevenly overlooked (Tuya et al., 2023). Considered foundation species (per Dayton, 1972 definition), rhodoliths are regarded as autogenic ecosystems engineers, as their morphological complexity increases the heterogeneity of the environment that they are part of, and favours the survival and settlement of different organisms (Jones, Lawton and Shachak, 1994). Moreover, the interstitial spaces within rhodoliths' skeletons are important microhabitats to diverse fauna and flora, and each individual can harbour spores and propagules of macro and microalgae at their endolithic portion, acting as "seedbanks" and being considered biodiversity hotspots (Amado-Filho, 2010; Peña et al., 2014; Ordines et al., 2015; Lundquist et al., 2017; Krayesky-Self et al., 2017; Fredericq et al., 2019; Veras et al., 2020). The habitats created by rhodoliths also represent significant nursery areas, serve as refuges from predation, and represent an important and underrated reef fish habitat (Jackson et al., 2004; Kamenos, Moore & Hall-Spencer, 2004; Meihoub Berlandi et al., 2012; Teichert, 2014; Prata et al., 2017; Moura et al., 2021). Besides their important ecological roles, rhodolith beds also are critical carbon sinks and play an important role in carbon budget (Amado-Filho et al., 2012; van der Heijden & Kamenos, 2015). Consequently, the presence of rhodolith beds increases local biodiversity, providing

and supporting multiple ecosystem services (Foster, 2001; Steller et al., 2003). Rhodolith beds are vulnerable to a set of anthropogenic activities, such as sedimentation, climate changes, dredging and anchoring, which can affect its structural complexity. Despite the ecological importance of these benthic environments, rhodolith associated cryptofauna remains unexplored, and there is no consensus about the main factors driving its faunal diversity and abundance (Steller & Cáceres-Martínez, 2009), as various and disagreeing responses have been encountered. Different morphologies have shown to influence cryptofauna community composition, such as volume/size and/or branch tips (Steller et al., 2003; Meihoub Berlandi et al., 2012; Mendéz Trejo et al., 2020), while no differences have been reported for species of distinct growth forms (Hinojosa-Arango & Riosmena-Rodríguez, 2004; Harvey & Bird, 2008). Some authors concluded that three-dimensional structure of rhodoliths is a key driver influencing its associated fauna (Steller et al., 2003; Otero-Ferrer et al., 2019). Also, physical environmental characteristics can indirectly influence rhodolith cryptofaunal composition (Abrecht et al., 2021). There is a lack of understanding about which aspects of rhodoliths tri-dimensional structure (likewise volume, size, diameter, sphericity, branch tips, free-volume space) are the main force driving complexity in a rhodolith nodule, as an attempt to quantify those characteristics is recent (Jardim et al., 2022), or if these structural complexity is the most important factor influencing cryptofaunal associated communities, or whether species-specific interactions are more significant, as chemical interactions between rhodoliths forming species and associated fauna may affect community structure (Steller and Cáceres-Martínez, 2009). Therefore, our aim was to evaluate the cryptofauna associated to two rhodolith forming species, *Lithophyllum atlanticum* (Vieira-Pinto, M.C Oliveira & P.A Horta 2008) e *Melyvonnea erubescens* ((Foslie) Athanasiadis & D.L Ballantine 2014). Both species co-occur in a rhodolith bed in the SW Atlantic, and have very different growth forms, following the standardized terminology elaborated by Woerkeing et al., 1993. *M. erubescens* exhibits a fruticose to warty morphology, its highly branched and has shorter protuberances (1.5 – 4 mm length, 1-2 mm diameter) (Sissini et al., 2014), regarded to *L. atlanticum* (5-10 mm length, 3.5 mm diameter), which exhibits a smooth or warty to lumpy surface regarded to its morphology (Vieira-Pinto et al., 2014). Here we described macroinvertebrate cryptofaunal community structure related to two rhodolith forming-species with different growth forms, and tested whether (1) structure

complexity; (2) depth and (3) seasons affect cryptofaunal community structure.

2. MATERIAL AND METHODS

2.1 Study area

The studied rhodolith bed is located in the SW Atlantic, inside of a Marine Protected Area off the coast of Santa Catarina state, named Reserva Biológica do Arvoredo (-27°16'25.8', -48°22'0.99'). This bed is located in a complex oceanographic scope, considering that in the summer the Brazilian Current (BC) is predominant (characterized by tropical warm waters and high salinity, coming from low latitudes), and in the winter, the Falklands Currents (FC) is stronger (with colder and less salty waters coming from high latitudes) (Matano et al., 2010; Orselli et al., 2018). FC interacts with Prata's River plume and diverse other freshwater sources, moving northward and reaching our study area (Möller et al., 2008; Strub et al., 2015).

A high biodiversity of macroalgae, zoanthids, ascidians, polychaetes, bivalves, crustaceans, ophiuroids, bryozoans and sponges has been reported associated to this rhodolith bed (Gherardi, 2004; Rocha et al., 2006; Horta et al., 2008; Riul et al., 2009; Scherner et al., 2010).

2.2 Sampling

We focused our sampling on rhodoliths of intermediate size, ranging from 45 to 83 mm, to guarantee that our measurements were not influenced by size, as previous studies have shown these interactions (Steller et al., 2003; McConnico et al., 2018). Rhodoliths were collected in two different depths, 2 and 9 m during spring (November 30, 2021); 4 and 9 m in the summer (February 17, 2022). The difference in depth of the shallower sampling points is due to variation in tidal movement. Five nodules of each species were collected from each depth. Rhodoliths were bagged individually for transport from the field to the laboratory, where they were stored in a freezer until transfer to flasks of 10% formaldehyde.

2.3 Cryptofauna

A total of 40 nodules were processed (20 *L. atlanticum* and 20 *M. erubescens*). Attached organisms were removed using pincers and chisels, and afterwards the individual rhodolith was broken and any internal cryptofauna was removed. All associated taxa > 0.5 mm were removed from between the branches, preserved in flasks of 10% formaldehyde, and identified to phylum.

2.4 Rhodoliths dimensions

Rhodolith volume was calculated according to the water displacement method. Rhodoliths' length, width and height were measured, and categorized in different shape classes as either discoidal, ellipsoidal, or spheroidal (Sneed & Folk, 1958). From the rhodoliths sphericity, by subtracting the volume of the ellipsoid from the volume of the rhodolith, the volume of free space between branches was obtained. This method allowed for the quantification of the available space within the rhodolith. Branching density was calculated by counting the number of branch tips in five randomly placed 1 cm² quadrats over the rhodolith surface (subset of three per species, each depth).

2.5 Statistical analysis

To describe the spatial distribution of samples, we utilized non-metric Multidimensional Scaling (nMDS). To test for the combined effects of seasons, depths and species on cryptofaunal biomass, we conducted a Permutational Multivariate Analysis of Variance (PERMANOVA). For both nMDS and PERMANOVA, we used similarity matrices based on the Bray-Curtis index, and the abundance values were square root transformed. The PERMANOVA analysis was performed on raw data with unrestricted permutations, using 999 random permutations for robust statistical inference. Same protocol was utilized for bottom samples, the only difference is that we suppressed data from shallower depths. We also performed a Distance-based Redundancy Analysis (DISTLM) to explore the relationship between environmental variables and the similarity matrix based on the Bray-Curtis index. Dataset used in the analysis consisted of multiple environmental variables and a Bray-Curtis similarity matrix. Prior

to analyses, we applied a log transformation to the resemblance data and a square root transformation to the environmental variables. Additionally, we normalized the environmental data. DISTLM analysis was conducted to examine how the environmental variables influenced the similarity patterns among the samples. The predictor variables included in the analysis were branches density, volume, free space volume, dry weight, season, and depths (last cited variable was excluded for bottom samples). We selected the best model based on the R^2 criterion, and the selection procedure involved specifying the variables to be included. We employed the Bray-Curtis index as the resemblance measure, and to assess the significance of the relationships, we performed 999 random permutations. Specific DISTLM test used was a Redundancy Analysis. PERMANOVA, nMDS and DISTLM were all performed at software PRIMER 6.0.

The community structure was described by the number of species, Shannon-Wiener diversity indices, and Pielou's evenness indices. To test possible differences between assemblages we performed a two-way ANOVA for variables that followed ANOVA assumptions, for those that did not follow these assumptions, Kruskal-Wallis were performed. When significant difference was observed, Duncan test was performed as post-hoc, Shapiro-Wilk test was utilized for normality, and Levene test for homoscedasticity. Plots depicting residuals versus fitted values were created to assess potential asymmetry or violations of model assumptions (Zuur et al., 2010). Those tests and box plot graphs were generated utilizing the "ggplot2" package in RStudio version 4.3.2.

3. RESULTS

3.1 Rhodolith structure

M. erubescens exhibits a higher volume of free space between branches and branch tips compared to *L. atlanticum*, both considering both species combined and at both depths. On the contrary, *L. atlanticum* displays a larger internal volume in comparison to *M. erubescens*. Furthermore, the data reveals that both volume and branch tips decrease as depth increases, while the opposite trend is observed for free space in both species (Table 1; S1).

Species	Depth	Volume (cm ³)	Free space (cm ³)	Branches (number/cm ²)
<i>M. erubescens</i>	2 m	77.6 ± 28.7	29.7 ± 17.5	10.8 ± 1.4
<i>M. erubescens</i>	9 m	62.6 ± 10.1	33.1 ± 21.9	7.3 ± 0.3
<i>M. erubescens</i>	Combined	70.1 ± 22.3	30.5 ± 19.6	9.1 ± 2.1
<i>L. atlanticum</i>	2 m	79.9 ± 14.6	23.2 ± 19.3	4.3 ± 0.7
<i>L. atlanticum</i>	9 m	66.9 ± 24.3	27 ± 19.4	4 ± 0.5
<i>L. atlanticum</i>	Combined	73.4 ± 20.6	29.9 ± 18.7	4.2 ± 0.5
Table 1. Rhodolith dimensions (means ± SE)				

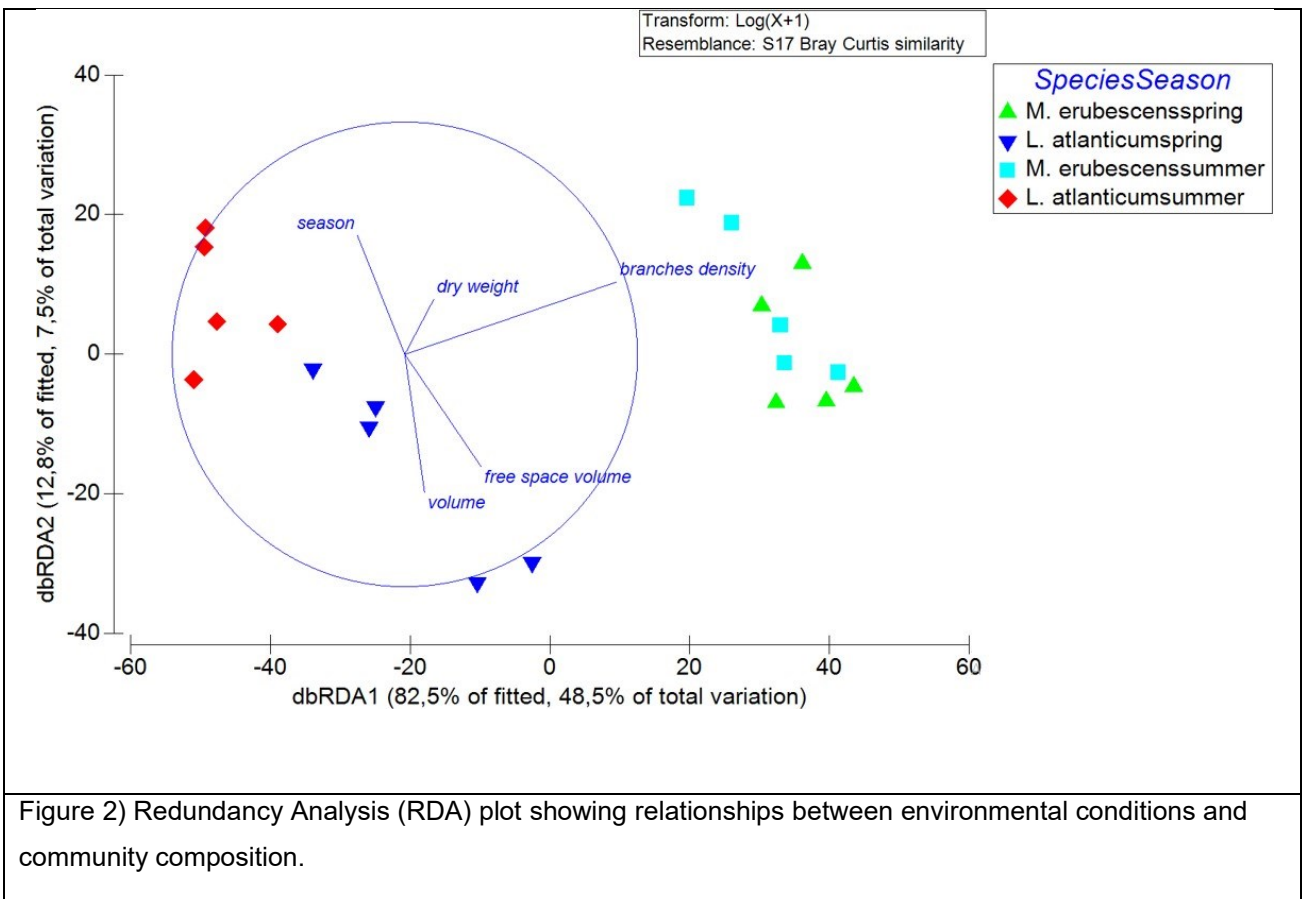
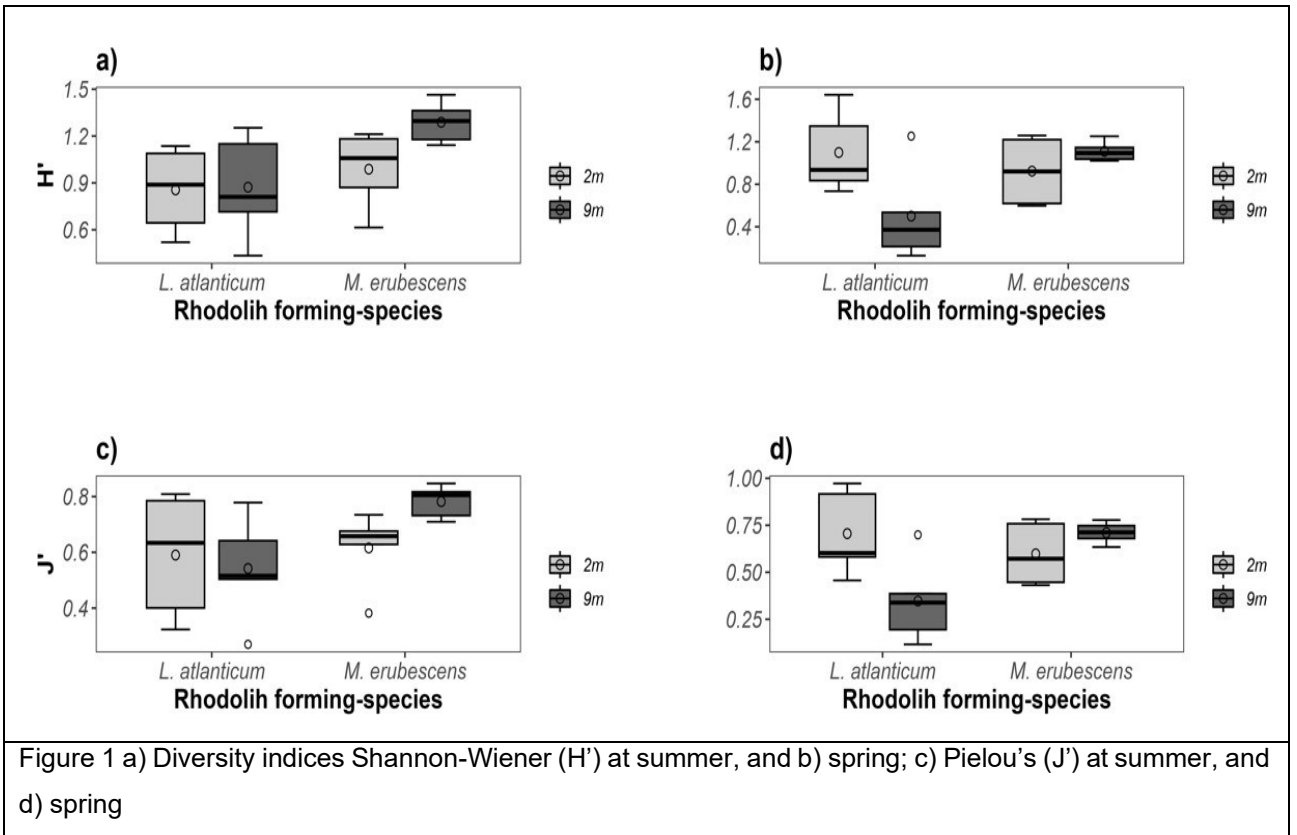
3.2 Species richness, biomass and diversity

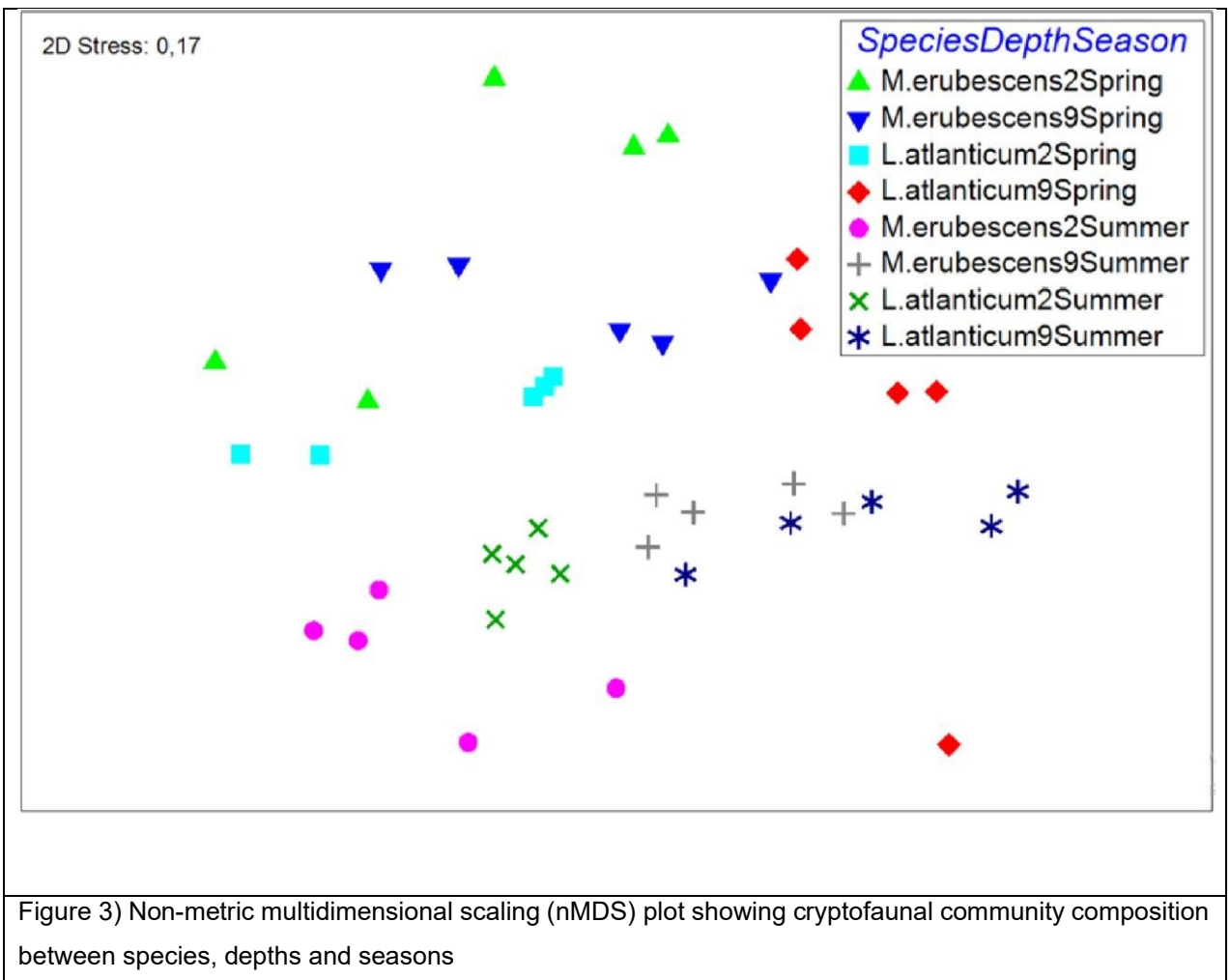
In the analysis of 40 rhodoliths nodules, a total of eight classes belonging to four different phyla (Annelida, Echinodermata, Mollusca, Arthropoda) were identified: Polychaeta, Sipunculids, Ophiuroidea, Crinoidea, Polyplacophora, Gastropoda, Bivalvia, Malacostraca (S2). Sipunculids is referred as class, considering recent replacement within the annelid radiation, based on phylogenetic and phylogenomic analyses (Boore and Staton, 2002; Telford, Wise and Gowri-Shankar, 2005; Dunn et al., 2008; Mwyni et al., 2009; Struck et al., 2009; Weigert et al., 2014; Weigert et al., 2016; Zhe Zheng et al., 2023). Considering richness and two different diversity indices: Shannon-Wiener diversity index (H'), which quantifies the overall diversity of species in a community, taking into account both species richness and evenness; and Pielou's evenness index (J'), which assess how evenly the individuals are distributed among different species in a community. No statistically significant difference for richness were observed ($p > 0.05$), although interesting trends are observed, within lowest number of species varying from 3 (in *L. atlanticum*) to 6 (in *L. atlanticum* and *M. erubescens*), and biomass increasing in *L. atlanticum* regarded to *M. erubescens*, in summer related to spring for both species and depths, and increasing for *L. atlanticum* at the bottom for both seasons, and decreasing for *M. erubescens* at both seasons) (S3). Pielou's evenness values varied from 0.11 to 0.97, and Shannon-Wiener diversity from 0.12 to

1.6 among the samples (S4). Shannon-Wiener indexes for summer showed differences between species ($p < 0.05$), post-hoc tests pointed differences between *M.erubescens* (9m) and *L. atlanticum* (2m); *M. erubescens* and *L. atlanticum* at 9 m. Shannon indexes at spring showed significant differences at interactions species/depth, post hoc comparisons shed light on *L. atlanticum* between 9m and 2m; and *M. erubescens* and *L. atlanticum* at 9m. Pielou's indexes for summer showed no differences, for spring significant differences were observed at species/depth, post-hoc analysis showed differences for *M. erubescens* and *L. atlanticum* at 9 m; *L. atlanticum* 2m and 9m; and *L.atlanticum* (9m) and *M.erubescens* (2m) (S5). As no difference was observed, to model analyses we suppressed the season factor.

3.3 Species composition

Cryptofaunal composition varied significantly for *M. erubescens* and *L. atlanticum*, considering depths ($p < 0.05$), post-hoc comparisons showed significant differences in composition between both depths. When species, depth and season combined, analysis found a significant difference too ($p < 0.05$). Pairwise tests were then undertaken, revealing significant differences at 9 meters samples at summer ($p < 0.05$) (Figure 3). No differences were found considering species and seasons ($p > 0.05$). As most substantial differences were observed in deeper areas, analysis performed considering samples collected at 9 meters, for both seasons, shows that composition differs from one species to another, within p-values < 0.05 for spring and summer (S6). General DISTLM considering all dataset does not show significant results, R^2 coefficient is low (17.58%), indicating that the predictor variables (branch density, volume, free space volume, dry weight, depth, and season) have little impact on the similarity among the samples. DISTLM for bottom sample analysis revealed that the environmental variables collectively explained a significant proportion of the variation in the resemblance matrix (58.75%) (Figure 2). Among the predictor variables, branch density showed the strongest association (p -value < 0.05), explaining 43.28% of the variation. Volume, free space volume, and dry weight also exhibited significant associations with resemblances patterns. Coordinate scores for each sample along the axes shows notably that branch density, volume, and free space volume variables had positive weights on Axis 1, indicating their strong influence on the similarity patterns (S7).





4. DISCUSSION

Community composition differs mainly at the bottom samples. Both rhodolith species display distinct structural characteristics in terms of free space, internal volume, and branch tips, with *M. erubescens* having more free space and much more branch tips abundance, and *L. atlanticum* having a larger internal volume. Depth seems to influence the structural attributes, as volume and branch tips decrease with increasing depth, while free space increases in both species. These findings shed light on the differences in the habitat characteristics of the two rhodolith forming species and their potential implications for associated cryptofaunal communities.

Volume in *L. atlanticum* is higher than in *M. erubescens*, which in turn has a little freer space and branch density. Those structural characteristics appear to influence our

cryptofaunal distribution analysed, as Polychaetes and Ophiuroidea relative abundance was particularly higher in *M. erubescens* than in *L. atlanticum*, likely due to the preference of these organisms to associate with the interstices of rhodoliths, despite that, other taxa like Sipunculids, Gastropoda, Bivalvia and Malacostraca, with different body characteristics and bigger size, seems to prefer *L. atlanticum*, which structurally differ from *M. erubescens* in volume. As both species holds high diversity compared to other studies, our results are in line with those which associate higher abundance or diversity to elevated internal complexity (Berlandi et al., 2012; Belanger et al., 2020; Mendez-Trejo et al., 2021) or volume/size (Steller et al., 2003).

Reduction in rhodolith volume with an increase in depth was observed by few previous studies (Steller and Foster, 1995; Riul et al., 2009; Amado-Filho et al., 2010; Bahia et al., 2010; Pascelli et al., 2013), and in accordance with Steller et al., 2013, which relates higher abundance as bigger volume/size of rhodoliths.

Environmental changes may have indirectly driven different community composition at the bottom, and as previously observed by Carvalho et al., 2020, benthic community variability is intricate, and rhodolith bed structure varies along different seasons, wind direction and speed can influence its distribution (Carvalho et al., 2020). Similar to previous studies, Annelids, Molluscs and Malacostraca (mainly Crustaceans) domain macrobenthic cryptofaunal assemblage (Birkett et al., 1998; De Grave et al., 2000; Hinojosa-Arango and Riosmena-Rodríguez, 2004; Figueiredo et al., 2007), here we encountered differences in cryptofaunal community composition, considering both species combined. Difference in cryptofaunal composition between two different species was also observed by Hinojosa-Arango and Riosmena-Rodríguez, 2004; Trejo et al., 2020, though Hinojosa-Arango and Riosmena-Rodríguez, 2004 in the same study compared two different growth forms from same rhodolith forming species and found no significant difference, same result observed by Harvey and Bird, 2008, which observed two different growth forms and species. Carvalho et al., 2020 found cryptofaunal biomass decreased at summer related to spring, for Annelida, Mollusca and Arthropoda (all-important cryptofaunal components also in our study), although in the sampling time (2015 spring and 2016 summer) there was an El Niño event, with atypical environmental conditions.

Lower rhodolith density is commonly been related to higher depths and high energy environments, and despite some observations that rhodolith density decreases with depth (Amado-Filho et al., 2007), Bahia et al. (2010) found that rhodoliths densities increased with depths in the northeast Brazilian coast, and Pascelli et al., 2013 observed in the same site of our study that rhodolith density decreased with depth in the winter, but increased in the summer, also in the same site, Riul et al., 2009 observed no variations for rhodolith densities related to depth. Observing parameters that confers complexity to rhodoliths habitats, Jardim et al. (2022) found that rhodolith density is one of the main metrics driving complexity, authors also have found that complexity in these environments can vary in very small spatial scale (200 m), considering these remarks, and as pointed by Sugihara and May, 1990, complexity increases as repetition of small structuring elements enhance. These affirmations could lead us to the conclusion that higher rhodoliths densities could favor the formation of a more complex portion in the rhodolith bed, which in turn and in our study can synergistically act with individual rhodolith structure and trophic dynamics, explaining differences regard to 9 meters depth, as structurally complex habitats provide more niches, hence more resources (MacArthur and MacArthur, 1961; Tews et al., 2004). Elements of rhodolith structure play a significant role in shaping the composition and distribution of cryptofaunal communities, as structural complexity is frequently considered a key factor driving biodiversity, which in turn influences the associated rhodoliths cryptofauna (Grall et al., 2006; Gabara et al., 2018; Otero-Ferrer et al., 2019). Apart from structural and/or environmental characteristics, important interactions regard morphology and chemical signals may occur too, and its reported being species-specific as length of protuberances increases the diffusive boundary layer, which dictates larger pH daily fluctuations gradients as DBL increases (Cornwall et al., 2014). *L.atlanticum* has thicker DBL as protuberances are longer than *M. erubescens* (Schubert et al., 2021), conferring differences between both species in chemical set ups at a microscale.

5. CONCLUSIONS

Despite no significant differences in diversity along seasons and depths for both species, the structural differences apparently played a crucial role in shaping the cryptofaunal distribution. Both species exhibited high diversity and supported a diverse assemblage of taxa, with differences in its composition regarded to their different growth forms and structural features. The habitat complexity created by these rhodolith-forming species likely supports the recruitment and survival of a wide range of associated organisms, making them important biodiversity hotspots. Our findings also indicate that environmental factors, such as depth and season may indirectly play a role in shaping the composition and distribution of cryptofaunal communities associated with rhodoliths. Further investigations should explore how variations in environmental conditions, such as currents and water quality, influence the dynamics of cryptofauna in rhodolith beds. Future research also should focus on understanding the ecological interactions between rhodolith-forming species and associated cryptofauna. Investigating the specific factors influencing species interactions and the functional roles of cryptofaunal communities in these habitats would enhance our understanding of the broader ecological significance of rhodolith beds. Overall, this study contributes with insights into the cryptofaunal diversity and community composition associated with rhodolith beds in the SW Atlantic, highlighting the ecological importance of these habitats and the need for further research to fully comprehend their ecological complexity and conservation implications. Besides, there is a bill proposing to change the no-take area studied to a more permissive area, raising concerns about the protection of sensitive areas such as rhodolith beds, in the face of potential impacts from the expansion of oil and gas industry in adjacent areas, also the increase in public visitation. Providing support for management decisions to properly preserve rhodolith beds and the no-take area is imperative to maintaining its biodiversity and ecosystem services.

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CONCLUSÃO GERAL

As diferenças estruturais aparentemente desempenharam um papel crucial na determinação da distribuição quali/quantitativa da criptofauna. Ambas as espécies apresentaram alta diversidade e sustentaram uma diversa assembléia de táxons, com diferenças em sua composição relacionadas às suas diferentes formas de crescimento e características estruturais. A complexidade do habitat criada por essas espécies formadoras de rodólitos provavelmente suporta o recrutamento e a sobrevivência de uma ampla variedade de organismos associados, tornando-os importantes pontos de biodiversidade. Nossos resultados também indicam que fatores ambientais, como profundidade e sazonalidade, podem desempenhar indiretamente um papel na formação da composição e distribuição das comunidades criptofaunais associadas aos rodólitos.

Investigações futuras devem explorar como variações nas condições ambientais, como correntes, qualidade da água, e temperatura, por exemplo, influenciam a dinâmica da criptofauna em bancos de rodólitos. Pesquisas futuras também devem focar na compreensão das interações ecológicas entre as espécies formadoras de rodólitos e a criptofauna associada. Investigar os fatores específicos que influenciam as interações entre espécies e os papéis funcionais das comunidades

criptofaunais nestes habitats aprimoraria nossa compreensão da importância ecológica mais ampla dos bancos de rodolitos.

No geral, este estudo contribui com informações sobre a diversidade e composição da comunidade criptofaunal associada ao banco de rodolito localizado no Rancho Norte, dentro da REBio Marinha do Arvoredo, no Atlântico Sudoeste, destacando a importância ecológica desses habitats e a necessidade de mais pesquisas para compreender totalmente sua complexidade e implicações para a conservação.

Além disso, a Reserva Biológica Marinha do Arvoredo está enfrentando uma proposta de mudança para a categoria de Parque Nacional Marinho, o que traria alterações significativas em sua gestão, permitindo o uso público, diferente da categoria atual de Reserva Biológica. Essa possível mudança levanta preocupações sobre a proteção de áreas sensíveis, como os bancos de rodolitos, que poderiam ficar mais vulneráveis a impactos potenciais, como a expansão da indústria de óleo e gás na região sul da Bacia de Santos, próxima à reserva. Além disso, o aumento da visitação pública, especialmente para mergulho recreativo, pode causar impactos negativos nos bancos de rodolitos, como ancoragem inadequada e coleta indevida. Portanto, é crucial conduzir estudos que demonstrem a importância desse ambiente e entendam suas principais influências nos serviços ecossistêmicos. Essas informações são essenciais para apoiar a gestão da área e enfrentar os desafios que surgem com a possível mudança de categoria da reserva. Garantir a proteção adequada dos bancos de rodolitos e do ecossistema da Reserva Biológica Marinha do Arvoredo é fundamental para preservar sua biodiversidade e os benefícios ambientais que ela oferece à sociedade.

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