

Article

Latitudinal Patterns and Macroalgal Diversity in Marine Protected Areas Along the Southwest Atlantic

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Abstract

Macroalgae provide key ecosystem services, forming habitats such as kelp and fucoid forests, rhodolith beds, and coralline reefs that sustain high biodiversity. However, multiple stressors, including climate change, harmful fishery practices, and pollution and coastal urbanization are driving macroalgal diversity loss and changing species composition and abundance. This study aims to assess macroalgal representativeness, richness and endemism in 16 Marine Protected Areas (MPAs), including four oceanic islands, and test if macroalgal assemblages in MPAs are distributed along a latitudinal gradient (0–29° S) in the Southwest Atlantic. To investigate the processes underlying community patterns, β -diversity was decomposition turnover and nestedness components. The complexity of taxonomic structure was measured by taxonomic distinctness. Overall, the studied MPAs comprised 695 macroalgal taxa, about 69% of Brazilian taxa, and 36% of the endemics. Rhodophyta were dominant (449 species) in most studied areas, except at Trindade and Martim Vaz Archipelago MPA, followed by Chlorophyta (158 species) and Ochrophyta (88 species). Macroalgal species composition in MPAs varied with latitude, and not with area size. They were continuously distributed across northeastern, eastern and southeastern Brazil and oceanic island ecoregions, between Fernando de Noronha (3° S) and São Paulo Litoral Norte (23° S) MPAs. Macroalgal diversity dissimilarity among MPAs was 92%,



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dominated by the turnover component (88%) and nestedness as a minor component (4%), indicating that dissimilarities are mainly driven by the replacement of species, rather than a gradual loss or gain of species. Effective protection of these MPAs should be prioritized as they harbor highly diverse, unique, and heterogeneous macroalgal assemblages along the SWA, surrounded by heavily impacted areas. Assessment of human impacts on macroalgal habitats in MPAs would contribute to defining effective management actions. Mid- and offshore shelf macroalgal habitats, particularly rhodolith beds, which harbor rare kelp species and mesophotic reefs, remain underprotected, and should be integrated into marine spatial planning for biodiversity conservation.

Keywords: beta-diversity; coral reefs; Southwest Atlantic; rhodolith beds; rocky shore; species assembly

1. Introduction

Macroalgae are highly diverse photosynthetic organisms classified into three phyla: Rhodophyta (red algae), Chlorophyta (green algae), Ochrophyta (brown algae). They play important ecological roles, including nutrient and carbon cycling, and provide food for millions of people worldwide [1]. Both tropical macroalgal meadows and temperate canopies support local fisheries by increasing fish biomass and diversity, functioning as nursery habitats, and contributing to food security [2]. Several macroalgal species are ecosystem engineers or foundation species [3], maintaining the resilience of marine ecosystems [4].

The increasing coastal degradation caused by pollution, habitat change, overfishing and invasive species, together with climate change, has threatened macroalgae globally [1,5]. Canopy-forming species are particularly affected by rising seawater temperatures, leading to coastal degradation through their replacement by turf algae [6]. Several non-geniculate coralline algal species (NGCA; *sensu* [7]) and the calcifying green algae *Halimeda* J.V.Lamouroux are threatened by elevated pCO₂ levels [8,9]. Despite their ecological importance and vulnerability to multiple threats, macroalgal species and the habitats they form remain largely overlooked in conservation policy and management planning [1,10]. Only 65 red seaweed species have been included in the International Union for the Conservation of Nature (IUCN) Red List so far, with 1.5% listed as Extinct, 9.2% as Critically Endangered, and 4.6% as Vulnerable. For brown seaweed, only 15 species are included in the IUCN Red List, with 26.5% as Critically Endangered, 6.5% as Endangered and 6.5% as Vulnerable, all threatened reported by climate change and extreme weather events (the IUCN Red List, v3.1).

The Brazilian coastline, with its reentrances, extends over 10,000 km [11] along the Southwest Atlantic (SWA) and forms the Blue Amazon, an area of 6,801,323.61 km² (680,132,361 ha), currently under ratification by the Commission on the Limits of the Continental Shelf (CLCS) [12]. This coastal and marine system is characterized by highly turbid and nutrient-rich waters [13], originating from the large estuarine plumes of the Amazon and Orinoco Rivers in the north, and Patos Lagoon and Plata River estuaries in the south, as well as numerous smaller estuaries along the coast (e.g., São Francisco River, Doce River). These coastal and marine ecosystems encompass three biogeographic provinces, the North Brazil Shelf, the Tropical Southwestern Atlantic and the Warm-Temperate Southwestern Atlantic, and eight marine ecoregions, including three oceanic islands and one atoll [14].

According to [15], four phycogeographical zones were first proposed along the coast, which were later [16] grouped into two major regions, a tropical region and a warm-temperate region, separated by a transitional zone. Recently, multi-taxa studies have demonstrated that species composition clearly varies along the latitude in the SWA [17,18]. Macroalgal diversity within Marine Protected Areas (MPAs) still remains poorly understood, as does their distribution along the SWA. Testing whether macroalgal assemblages in MPAs follow a latitudinal distributional pattern (e.g., latitude vs. area) and understanding the processes that produce this pattern are essential for assessing these MPAs and their importance for biodiversity conservation.

In Brazil, macroalgae (turf and fleshy algae) dominate benthic marine communities [19] such as shallow and deep biogenic reefs and rocky shores. In SWA, coral reefs are known as marginal reefs (according to the definition in [20]), because they thrive under elevated turbidity and high sedimentation, and show low coral cover, high endemism and high turf algae and macroalgal cover [19,21–23]. Mesophotic reefs, extending along the Amazon Continental Margin and Abrolhos Bank, form part of the SWA coralline seascape [23,24]. Rhodolith beds comprise the world's largest continuous area on the Abrolhos Bank [25], and also occur discontinuously across the mid- to offshore shelf, representing the largest mesophotic habitat [26]. Brazilian kelps are associated with rhodoliths and are dominated by the endemic *Laminaria abyssalis* A.B.Joly & E.C.Oliveira, which occur in a restricted deep-water habitat that is currently under threat [27,28]. These kelp–rhodolith systems, as well as rhodolith beds in general, remain poorly protected [29,30].

This study aims to (1) assess macroalgal representativeness, richness and endemism in 16 MPAs, including three oceanic archipelagos and one atoll, that include biodiversity hotspots distributed across eight Brazilian ecoregions; (2) test whether macroalgal assemblages in MPAs follow a latitudinal gradient, or are structured into two major phycogeographical zones (tropical and warm-temperate); (3) explore potential processes underlying species composition patterns among MPAs through β -diversity decomposition; and (4) assess the complexity of the taxonomic structure and diversification process using Taxonomic Distinctness Average ($\Delta+$) and Taxonomic Distinctness Variation ($\Delta+$). We also discuss possible implications of our findings for MPAs conservation and management.

2. Materials and Methods

2.1. Marine Protected Areas

Currently, Brazil has 233 MPAs: 78 federal areas (31 no-take and 47 multiple-use) covering 92,651,612 ha; 92 MPAs are under state administration (32 no-take and 60 multiple-use) totaling 4,185,577 ha; and 63 are managed by municipalities. In this study, 16 MPAs distributed across all Brazilian ecoregions were analyzed: (1) Parcel de Manuel Luís Marine State Park, (2) São Pedro and São Paulo Archipelago Natural Monument and Environmental Protected Area, (3) Fernando de Noronha National Park, (4) Rocas Atoll Biological Reserve, (5) Recifes de Corais Environmental Protected Area, (6) Costa dos Corais Environmental Protected Area, (7) Baía de Todos os Santos Environmental Protected Area, (8) Abrolhos Marine National Park, (9) Trindade and Martim Vaz e do Monte Columbia Natural Monument and Trindade and Martim Vaz Archipelago Environmental Protected Area, (10) Costa das Algas Environmental Protected Area, (11) Arraial do Cabo Marine Extractive Reserve, (12) Tamoios Ecological Station, (13) Litoral Norte São Paulo Marine Environmental Protected Area, (14) Area of Relevant Ecological Interest Queimada Pequena and Queimada Grande Islands, (15) Arvoredo Marine Biological Reserve, and (16) Lobos Island Wildlife Refuge (Figure 1; Table 1; Supplementary Material S1—Table S1).

Table 1. Characteristics of Marine Protected Areas (MPAs) (Figure 1, Supplementary Material S1—Table S1) (*) [14].

No.	Marine Protected Area	Ecoregion (*)	State	Management	Date of Creation
1	Parcel de Manuel Luís Marine State Park	Amazonia	Maranhão	No-take	11 June 1991
2	São Pedro and São Paulo Archipelago Natural Monument and Environmental Protected Area	São Pedro and São Paulo Islands	Rio Grande do Norte	No-take/Multiple-use	19 March 2018
3	Fernando de Noronha National Park	Fernando de Noronha and Atoll das Rocas	Pernambuco	No-take	15 September 1988
4	Rocas Atoll Biological Reserve	Fernando de Noronha and Atoll das Rocas	Rio Grande do Norte	No-take	5 June 1979
5	Recifes de Corais Environmental Protected Area	Northeastern Brazil	Rio Grande do Norte	Multiple-use	6 June 2001
6	Costa dos Corais Environmental Protected Area	Northeastern Brazil	Pernambuco and Alagoas	Multiple-use	23 October 1997
7	Baía de Todos os Santos Environmental Protected Area	Eastern Brazil	Bahia	Multiple-use	6 September 1999
8	Abrolhos Marine National Park	Eastern Brazil	Bahia	No-take	6 April 1983
9	Trindade and Martim Vaz and Mount Columbia Natural Monument and Trindade and Martim Vaz Archipelago Environmental Protected Area	Trindade and Martim Vaz Islands	Espírito Santo	No-take/Multiple-use	10 March 2018
10	Costa das Algas Environmental Protected Area	Eastern Brazil	Espírito Santo	Multiple-use	17 June 2010
11	Arraial do Cabo Marine Extractive Reserve	Southeastern Brazil	Rio de Janeiro	Multiple-use	3 January 1997
12	Tamoios Ecological Station	Southeastern Brazil	Rio de Janeiro	No-take	23 January 1990
13	Litoral Norte São Paulo Marine Environmental Protected Area	Southeastern Brazil	São Paulo	Multiple-use	9 October 2008
14	Area of Relevant Ecological Interest Queimada Pequena and Queimada Grande Islands	Southeastern Brazil	São Paulo	Multiple-use	5 November 1985
15	Arvoredo Marine Biological Reserve	Southeastern Brazil	Santa Catarina	No-take	13 March 1990
16	Lobos Island Wildlife Refuge	Rio Grande	Rio Grande do Sul	No-take	4 April 1983

These 16 MPAs were selected based on their biodiversity importance, ecoregion representation [14], and the availability of inventories. Most of them participate in long-term national and international monitoring programs [e.g., Global Environmental Facility—GEF Mar: MPAs (1), (2), (3), (4), (6), (8) and (16)], which facilitate data reliability and comparability. In addition, selection considered the inclusion of distinct habitat types (e.g., coral reefs, rhodolith beds, rocky shores, and oceanic islands), and their role in supporting fisheries and local livelihoods: MPAs (5), (6), (7), (10), (11) and (13). Many of the chosen areas are internationally recognized for their ecological significance—Ramsar Sites: (1), (3), (4), (8); UNESCO World Heritage Sites: (3) and (4); and UNESCO Atlantic Forest

Biosphere Reserve (RBMA) zones: (3)–(8) and (10)–(16). Together, these criteria ensured a representative and ecologically meaningful set of MPAs, spanning the full latitudinal range of the Brazilian coast and including both no-take and multiple-use categories (Table 1, Supplementary Material S1—Table S1).

These MPAs also encompass unique geomorphological and ecological features. In the Amazonia ecoregion, the Manuel Luis reefs consist of pinnacles 25–30 m deep, with their tops reaching up 2 m [23]. Fernando Noronha is the largest Brazilian oceanic archipelago, composed of 21 islands and islets of volcanic origin that harbor abundant coral fauna. Rocas Atoll developed on a flat top of a seamount, forming a reef ring open on its western and northern sides, built mainly by coralline algae [23]. In the tropical SWA, marginal reefs occur along the Brazilian northeastern coast. The Abrolhos Bank, a shelf enlargement, harbors the richest and the most well-known coral reefs [31]. These formations are mainly built by non-coral calcifiers as coralline algae and/or bryozoans [32]. The Trindade and Martin Vaz Archipelago, located 1200 km off the land, consisted of rocky islands [23], whose tops are dominated by rhodolith beds [33,34]. Ecologically relevant rhodolith aggregations have been mapped in the Costa das Algas MPA, the largest protected rhodolith bed in Brazil [35]. These formations resemble typical Mediterranean coralligenous reefs, formed by very complex and unique structures [36]. Further south along the Brazilian coast, rocky shores are a conspicuous feature, extending across the southwestern Brazil ecoregion [37]. Among them, the Arraial do Cabo MPA is distinguished for its high biodiversity, including unique articulith bed formations, free-living structures formed by geniculate coralline algae [38].

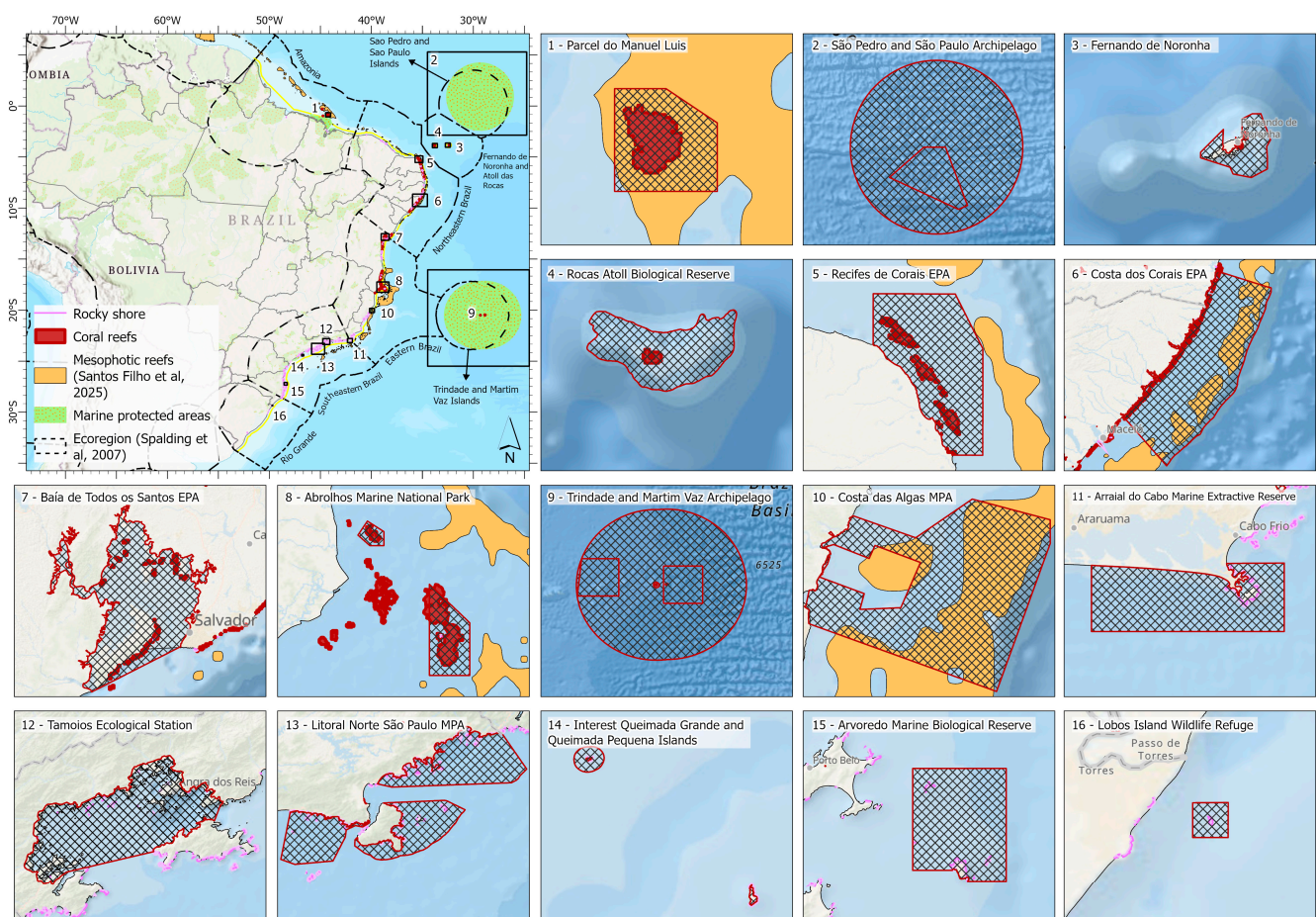


Figure 1. Location of the studied Marine Protected Areas (MPAs) (black grids) across the Brazilian ecoregions [14] in benthic ecosystems, coral reefs [39], mesophotic reefs [24], and rocky shores [40] in

the Southwest Atlantic (SWA). The map was generated using ArcGIS Pro v3.5.3. Red contours correspond to the studied MPAs. 1. Parcel de Manuel Luís Marine State Park, 2. São Pedro and São Paulo Archipelago Natural Monument and Environmental Protected Area, 3. Fernando de Noronha National Park, 4. Rocas Atoll Biological Reserve, 5. Recifes de Corais Environmental Protected Area, 6. Costa dos Corais Environmental Protected Area, 7. Baía de Todos os Santos Environmental Protected Area, 8. Abrolhos Marine National Park, 9. Trindade and Martim Vaz e do Monte Columbia Natural Monument and Trindade and Martim Vaz Archipelago Environmental Protected Area, 10. Costa das Algas Environmental Protected Area, 11. Arraial do Cabo Marine Extractive Reserve, 12. Tamoios Ecological Station, 13. Litoral Norte São Paulo Marine Environmental Protected Area, 14. Area of Relevant Ecological Interest Queimada Pequena and Queimada Grande Islands, 15. Arvoredo Marine Biological Reserve, 16. Lobos Island Wildlife Refuge.

2.2. Data Collection

Data were obtained from the Jabot (<http://www.jbrj.gov.br/jabot>, accessed on 14 December 2025) and Specieslink (<https://specieslink.net/>, accessed on 14 December 2025) databases, as well as from national herbaria (FLOR, HRJ, RB, SP, SPF), checklists in books, scientific journals and Ph.D. theses (see Supplementary Material S2—List S1 for the full list of references). Taxon names and their taxonomic classifications were updated following [41,42]. Final lists for each MPA were validated by recognized taxonomists, which resulted in an updated taxon list based on molecular taxonomic studies of Brazilian flora (Supplementary Material S1—Table S2). Checklists from 14 MPAs with available vouchers were published in the online Catálogo de Plantas das Unidades de Conservação do Brasil (<https://catalogo-ucs-brasil.jbrj.gov.br/>, accessed on 14 December 2025; Supplementary Material 2—List S2 for the references). For data compiled from oceanic island MPAs, the entire area was considered, including both no-take and multiple-use MPAs of the São Pedro and São Paulo and Trindade and Martin Vaz Archipelagos (Figure 1). In addition, a Brazilian macroalgal list was compiled from Flora e Funga do Brasil (<http://floradobrasil.jbrj.gov.br/>, accessed on 14 December 2025) and [42].

2.3. Data Analyses

All analyses were based on the presence and absence data from the 16 MPAs. After compiling all taxa into a single list, their frequency of occurrence across MPAs was assessed as very common (VC, ≥ 10 records); common ($5 \leq C \leq 9$ records); uncommon ($2 \leq UC \leq 4$); and rare (R, one record).

We investigated patterns of taxonomic dissimilarity in relation to latitude and Marine Protected Area (MPA) size. To this end, we employed the coefficient Γ^+ of taxonomic dissimilarity [43]. This coefficient was used because it provides greater robustness to taxonomic errors compared with conventional P/A metrics [43]. An additional advantage is that macroalgal assemblages can be analyzed across a broad geographic area, even when there are no shared species. To test the hypotheses of latitudinal changes and MPA size effect over taxonomic dissimilarity, we used an ordered non-parametric ANOSIM test, considering latitude and area as ordered factors [44]. This technique allows testing specific models for continuous variables such as latitude and size of the MPA. Non-metric multidimensional scaling (nMDS) plots were generated to visualize patterns of taxonomic dissimilarities among MPAs [43]. These analyses were carried out using the software PRIMER v7 [45].

To distinguish the processes responsible for latitudinal patterns, β -diversity (estimated using the Jaccard coefficient) was decomposed into two additive components that represent two opposing ecological processes: (a) spatial turnover of species, or replacement of species, which may result from niche partitioning, and (b) nestedness, or species loss along a gradient, potentially caused by dispersal capabilities or physiological limitations [46]. This

analysis was performed with the R package ‘betapart’ v 1.6.1 [47]. β -diversity is strongly coupled with α -diversity, which allows us to make inferences about the possible drivers of β -diversity [48]. We sought to evaluate changes in assemblage taxonomic structure across the latitudinal gradient. The metrics used, Average Taxonomic Distinctness ($\Delta+$) and Variation in Taxonomic Distinctness ($\Lambda+$) [49], serve as proxies for the relative roles of ecological, evolutionary, and historical processes in shaping latitudinal patterns [17]. According to [50], a high $\Delta+$ in the south region could indicate the existence of more evolutionary novelties (i.e., clades), supporting historical biogeographical hypotheses or higher speciation rates or lower extinction rates. To this end, $\Delta+$ and $\Lambda+$ were calculated separately for each phylum using PRIMER v7 [45]. These indices are dimensionless measures of taxonomic relatedness that assume the that Linnean classification reflects phylogenetic relationships. They represent the expected taxonomic path length between two randomly selected species in each MPA. The scale for these metrics is constructed by assigning branch lengths (ω) to the links between the hierarchical taxonomic levels used (Species, Genus, Family, and Order), assuming equal step lengths (or constant increments) between these successive levels [51]. The absence of trends across the latitudinal gradient suggests that local ecological constraints (e.g., niche partitioning) dominated over diversification linked to latitudes.

Graphs were produced in GraphPad v9.0.0, and nMDS were generated by PRIMER v7.

3. Results

3.1. Macroalgal Composition of MPAs

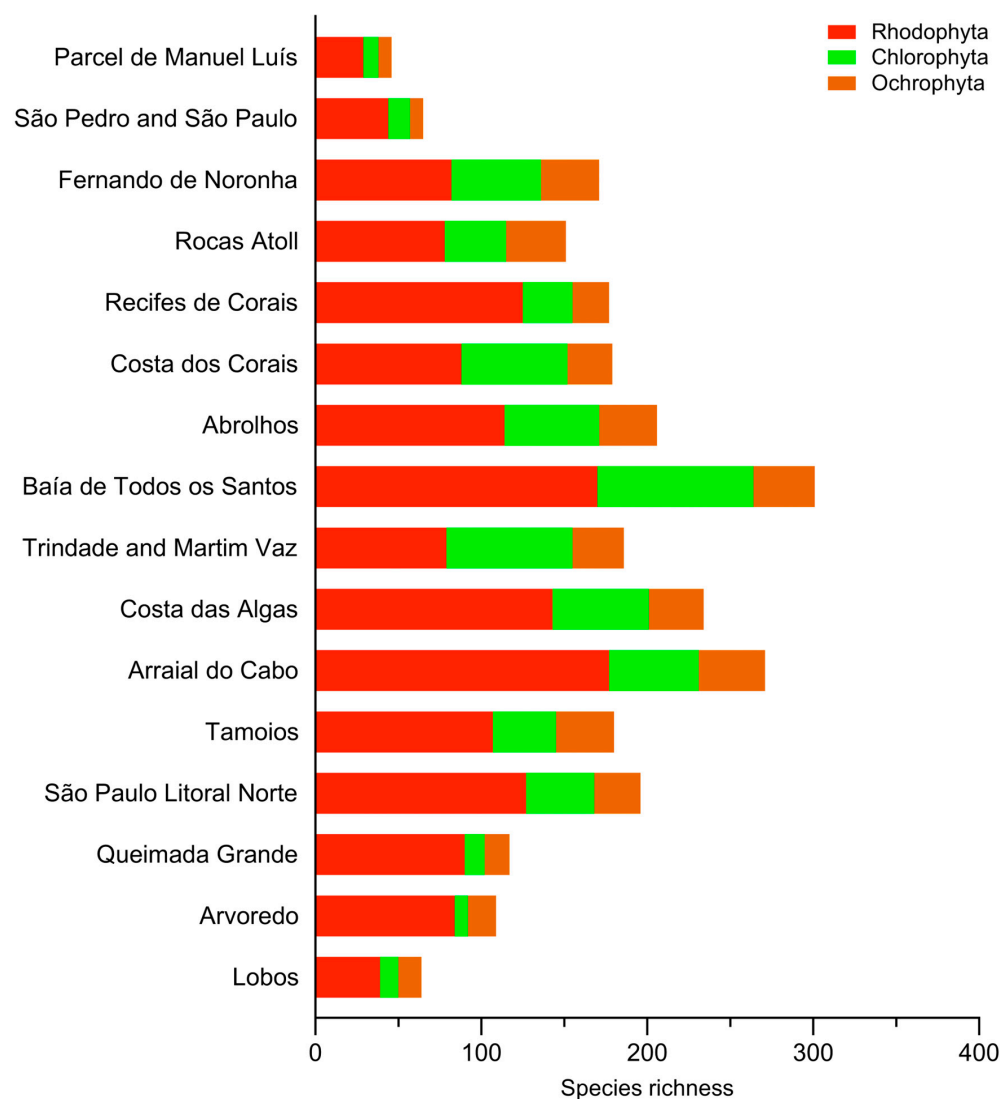
The compiled list of macroalgae from the 16 MPAs comprised 695 species (Supplementary Material S1—Table S3), representing ~69% of the 1009 taxa recorded in Brazil, including new records for the Brazilian flora. Rhodophyta was the richest phylum, with 45 families, 170 genera, 449 species (65% of MPAs total species); Chlorophyta consisted of 20 families, 45 genera, and 158 species (23%), and Ochrophyta comprised 13 families, 37 genera and 88 species (12%). The most species-rich families were Rhodomelaceae (87 species), Delesseriaceae (35) and Ceramiaceae (34) in Rhodophyta; Cladophoraceae (38) and Caulerpaceae (25) in Chlorophyta; and Dictyotaceae (36) in Ochrophyta.

Overall, most taxa in MPAs were rare (251, one record), or common (212 species), and 55 taxa were recorded in more than 10 MPAs. The most common macroalgae were, for red algae, *Asparagopsis taxiformis* (Delile) Trevisan, *Centroceras gasparrinii* (Meneghini) Kützinger, *Jania penduculata* var. *adhaerens* (J.V.Lamouroux) A.S.Harvey, Woelkerling & Reviere, *Gelidium microdenticum* W.R.Taylor, *Amphiroa beauvoisii* J.V.Lamouroux and *Laurencia dendroidea*; for green algae, *Bryopsis pennata* J.V.Lamouroux, *B. plumosa* (Hudson) C. Agardh, and *Ulva lactuca* Linnaeus; for brown algae, *Canistrocarpus cervicornis* (Kützinger) De Paula & De Clerck, *Dictyopteris delicatula* J.V.Lamouroux, *Lobophora variegata* (J.V.Lamouroux) Womersley ex E.C.Oliveira, and *Sargassum natans* (Linnaeus) Gaillon; J. Agardh. Twenty-six species (36%) are endemic, out of 72 endemics listed for Brazil. Most of the endemics recorded are Rhodophyta (22 taxa). The highest number of endemics (11) was recorded in the Costa das Algas MPA, located on the Espírito Santo shelf (Table 2).

Species richness in MPAs was highest at mid-latitudes (13–23° S) within the tropical–subtropical transition, including the Baía de Todos os Santos, the Costa das Algas, and the Arraial do Cabo MPAs (Figure 2). Richness declined toward both the northern (Parcel de Manuel Luís MPA, Amazonia ecoregion) and southern ends (Lobos Island MPA, Rio Grande ecoregion).

Table 2. Species richness of Rhodophyta, Chlorophyta and Ochrophyta and endemism in Marine Protected Areas (MPAs). MPAs are numbered from north to south.

No.	MPA	Latitude (°S)	Rhodophyta (% Total)	Chlorophyta (% Total)	Ochrophyta (% Total)	Total (% Total)	Endemic
1	Parcel de Manuel Luís	0	29 (63)	9 (20)	8 (17)	46 (7)	2
2	São Pedro and São Paulo	0	44 (68)	13 (20)	8 (12)	65 (9)	1
3	Fernando de Noronha	3	82 (48)	53 (32)	35 (20)	170 (24)	4
4	Rocas Atoll	3	78 (52)	37 (25)	36 (24)	151 (22)	3
5	Recifes de Corais	5	125 (71)	30 (17)	22 (12)	177 (25)	6
6	Costa de Corais	9	87 (49)	64 (36)	27 (15)	178 (26)	7
7	Baía de Todos os Santos	13	170 (56)	94 (31)	37 (12)	301 (43)	7
8	Abrolhos	17	114 (55)	57 (28)	35 (17)	206 (30)	7
9	Trindade and Martim Vaz	20	79 (42)	76 (41)	31 (17)	186 (28)	5
10	Costa das Algas	20	143 (61)	57 (25)	33 (14)	234 (34)	11
11	Arraial do Cabo	22	176 (65)	54 (20)	40 (15)	270 (39)	7
12	Tamoios	23	107 (59)	38 (21)	35 (19)	180 (26)	3
13	Litoral Norte São Paulo	23	126 (65)	41 (21)	28 (14)	195 (28)	6
14	Queimada Grande	24	89 (78)	11 (9)	15 (13)	115 (16)	5
15	Arvoredo	27	84 (77)	8 (7)	17 (16)	109 ((15)	4
16	Lobos	29	39 (61)	11 (11)	14 (22)	64 (9)	1

**Figure 2.** Species richness of Rhodophyta, Chlorophyta, and Ochrophyta in MPAs along the latitudinal gradient (Table 2).

Rhodophyta had the highest species richness among all MPAs (42–78%, Table 2, Figure 2), except in the Trindade and Martim Vaz MPA, where red and green species were equally dominant. Chlorophyta was the second species-rich group (7–41%), except in the three southernmost MPAs (Queimada Grande, Arvoredo and Lobos Island MPAs), where Ochrophyta was more diverse than green macroalgae (11–13%).

3.2. Latitudinal Patterns of Taxonomic Dissimilarity

Macroalgal species composition differed across latitudes (ANOSIM, $R = 0.514$, $p = 0.001$) but not with areas (ANOSIM, $R = 0.102$, $p < 0.183$). The Parcel de Manuel Luís MPA (1; Amazonia ecoregion), the oceanic São Pedro and São Paulo Archipelago MPA (2; São Pedro and São Paulo Islands ecoregion) and the southernmost coastal MPA, Lobos Island (16; Rio Grande ecoregion), were more distinct (Figure 3). Four tropical reef MPAs (5, 6, 7 and 10) in the northeastern and eastern Brazil ecoregions were more similar. Likewise, the nearby subtropical coastal rocky shore MPAs (Arraial do Cabo, Tamoios and São Paulo Litoral Norte) were also more similar, and together with tropical MPAs, followed a larger distribution from Fernando de Noronha (3° S) to São Paulo Litoral Norte (23° S). They differed from two southern areas (Queimada Grande (14) and Arvoredo Island (15) MPAs) in the southeastern Brazil ecoregion. The oceanic MPAs, Rocas Atoll (4) and Trindade and Martim Vaz Archipelago (9) and Abrolhos (8), were more similar to each other and did not follow a latitudinal pattern.

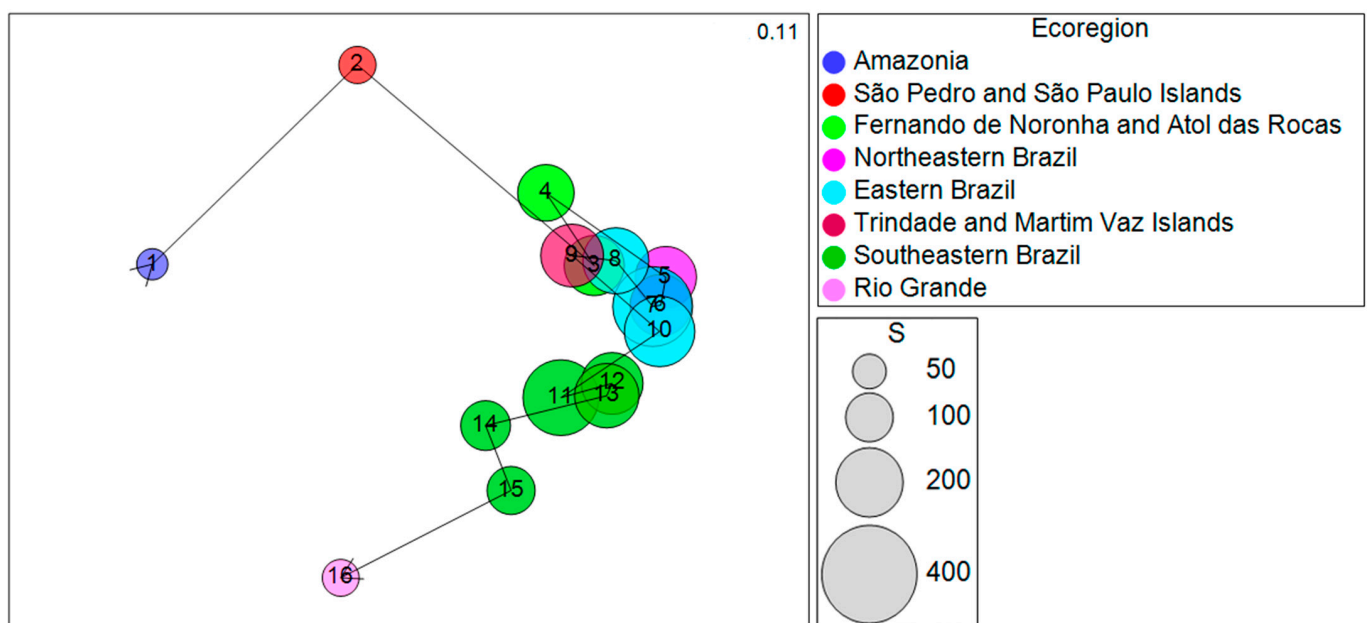


Figure 3. Non-metric multidimensional scaling (nMDS) (stress = 0.11) of species composition in Marine Protected Areas (MPAs) along a latitudinal gradient across ecoregions [14]. S indicates species richness; MPAs are numbered from north to south: 1. Parcel de Manuel Luís Marine State Park, 2. São Pedro and São Paulo Archipelago Natural Monument and Environmental Protected Area, 3. Fernando de Noronha National Park and Environmental Protected Area, 4. Rocas Atoll Biological Reserve, 5. Recifes de Corais Environmental Protected Area, 6. Costa dos Corais Environmental Protected Area, 7. Baía de Todos os Santos Environmental Protected Area, 8. Abrolhos Marine National Park, 9. Trindade and Martim Vaz e do Monte Columbia Natural Monument and Trindade and Martim Vaz Archipelago Environmental Protected Area, 10. Costa das Algas Environmental Protected Area, 11. Arraial do Cabo Marine Extractive Reserve, 12. Tamoios Ecological Station, 13. Litoral Norte São Paulo Marine Environmental Protected Area, 14. Area of Relevant Ecological Interest Queimada Pequena and Queimada Grande Islands, 15. Arvoredo Marine Biological Reserve, 16. Lobos Island Wildlife Refuge.

For Rhodophyta, species composition differed across latitudes (ANOSIM, $R = 0.474$, $p < 0.0001$). Assemblages from twelve MPAs were more similar to each other (Figure 4) than to the overall flora, following a broader latitudinal gradient that included the southern MPAs of Queimada Grande and Arvoredo in the southeastern ecoregion. However, the Abrolhos MPA did not follow this gradient, being more similar to the oceanic archipelago, Fernando de Noronha MPA (3), which was located further north. The Arraial do Cabo MPA was also similar to the Queimada Grande and Arvoredo MPAs.

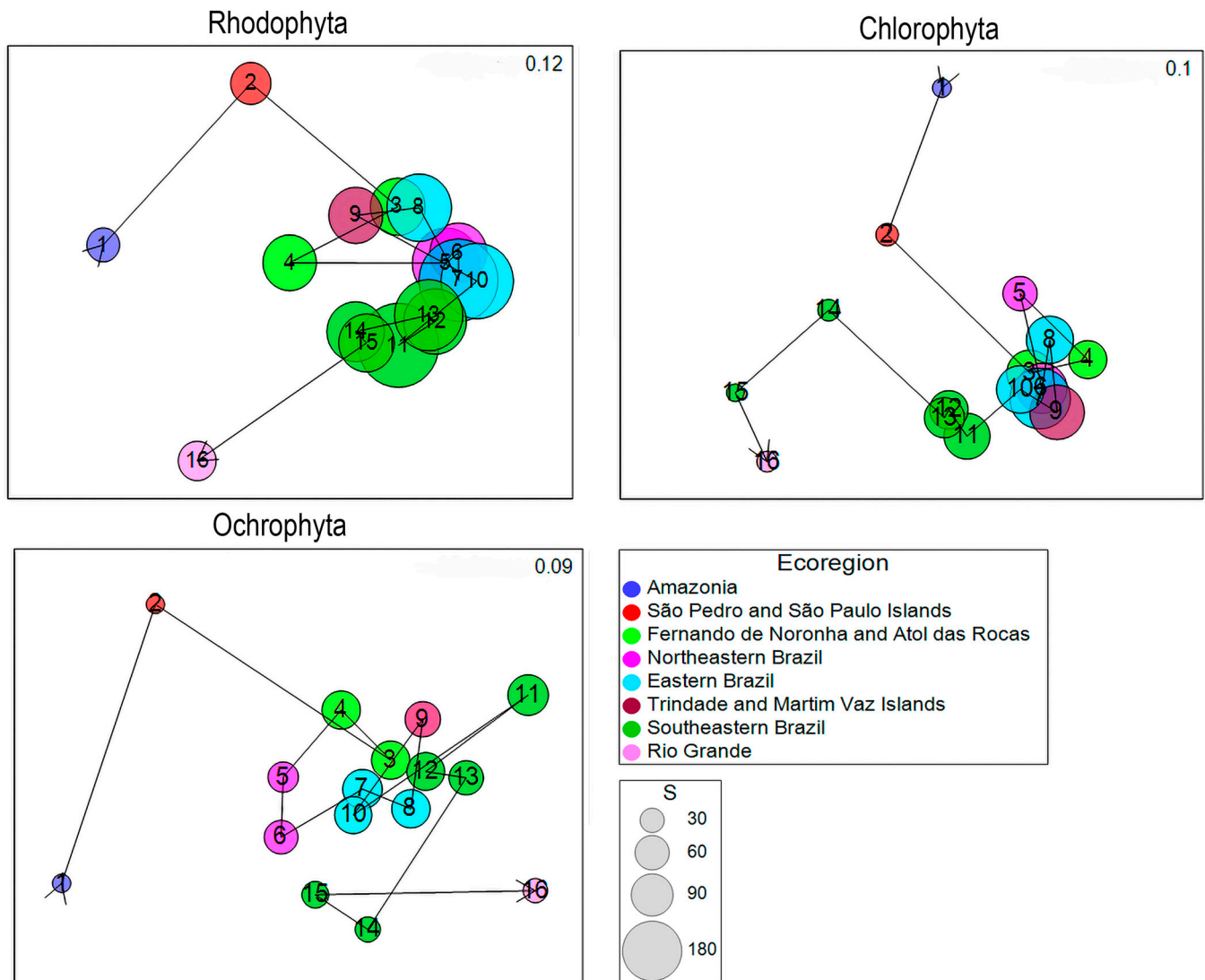


Figure 4. Non-metric multidimensional scaling (nMDS) of Rhodophyta (stress = 0.12), Chlorophyta (stress = 0.10) and Ochrophyta (stress = 0.09) species composition in Marine Protected Areas (MPAs) along a latitudinal gradient across ecoregions [14]. S indicates species richness; MPAs are numbered from north to south: 1. Parcel de Manuel Luís Marine State Park, 2. São Pedro and São Paulo Archipelago Natural Monument and Environmental Protected Area, 3. Fernando de Noronha National Park and Environmental Protected Area, 4. Rocas Atoll Biological Reserve, 5. Recifes de Corais Environmental Protected Area, 6. Costa dos Corais Environmental Protected Area, 7. Baía de Todos os Santos Environmental Protected Area, 8. Abrolhos Marine National Park, 9. Trindade and Martim Vaz e do Monte Columbia Natural Monument and Trindade and Martim Vaz Archipelago Environmental Protected Area, 10. Costa das Algas Environmental Protected Area, 11. Arraial do Cabo Marine Extractive Reserve, 12. Tamoios Ecological Station, 13. Litoral Norte São Paulo Marine Environmental Protected Area, 14. Area of Relevant Ecological Interest Queimada Pequena and Queimada Grande Islands, 15. Arvoredo Marine Biological Reserve, 16. Lobos Island Wildlife Refuge.

For Chlorophyta, species composition also differed across latitudes (ANOSIM, $R = 0.531$, $p < 0.0001$). Nevertheless, as observed in Rhodophyta, the tropical MPAs (Northeastern and Eastern Brazil, Fernando de Noronha and Atoll das Rocas, and Trindade and Martim Vaz ecoregions) were similar to each other, as were the southern coastal rocky shore MPAs (Arraial do Cabo, Tamoios and São Paulo Litoral Norte) (Figure 4). However, the two southernmost coastal islands, Queimada Grande and Arvoredo MPAs, were distinct from each other and from all other MPAs.

For Ochrophyta, species composition differed significantly with latitude (ANOSIM, $R = 0.382$, $p < 0.0001$). However, MPAs did not follow the same trend, and did not form a latitudinal gradient, being more distinct from each other. MPAs from the Eastern Brazil ecoregion (7, 8 and 10) were more similar to southern coastal areas, Tamoios and São Paulo Litoral Norte MPAs (12 and 13), than to those in the tropical northeastern Brazil ecoregion (5 and 6) (Figure 4). The nearby Arraial do Cabo MPA (11) was clearly separated from all other MPAs, as well as from the oceanic Rocas Atoll MPA (4).

Macroalgal assemblage dissimilarity among MPAs, based on the Jaccard index, was high (92%), with turnover as the dominant component (88%) and nestedness contributing only a small proportion (4%) [46]. Dissimilarity was largely driven by the replacement of species, rather than gradual species loss. Turnover varied significantly across latitudes (ANOSIM, $R = 0.3780$; $p < 0.001$). The nMDS of turnover (Figure 5) revealed a clear separation among all MPAs, indicating the replacement of species along the latitudinal gradient.

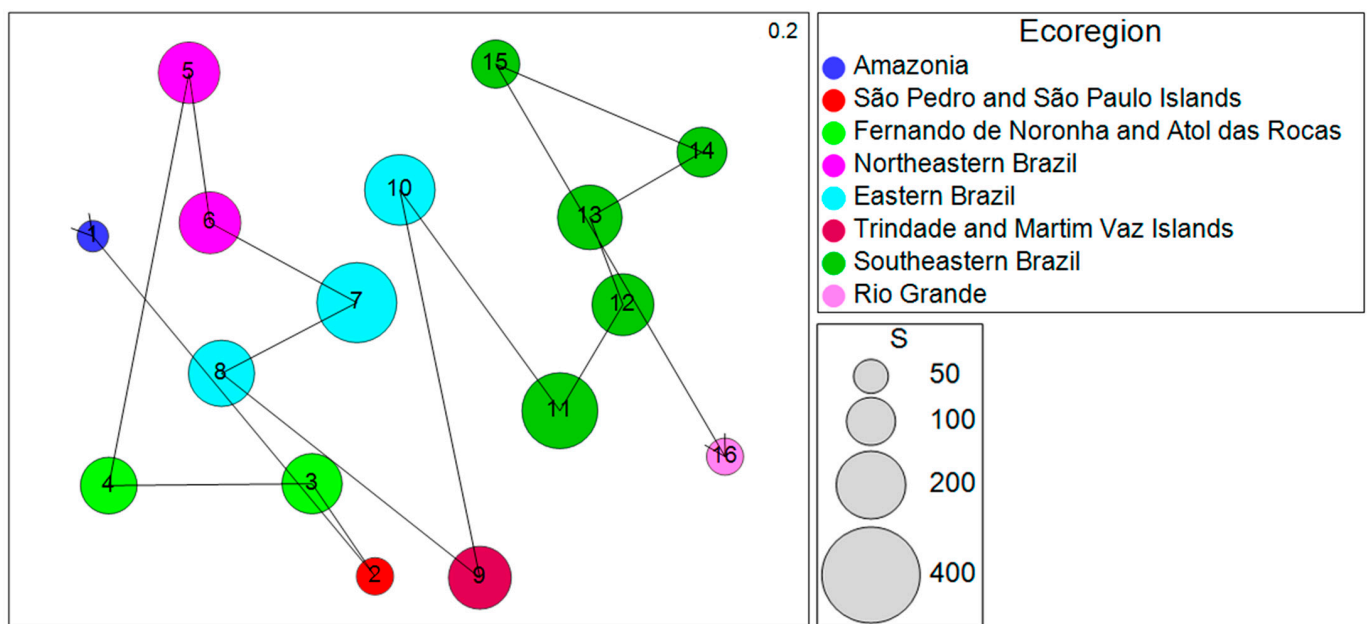


Figure 5. Non-metric multidimensional scaling (nMDS) (stress = 0.20) of turnover [46] in Marine Protected Areas (MPAs) along a latitudinal gradient across ecoregions [14]. S indicates species richness; MPAs are numbered from north to south: 1. Parcel de Manuel Luís Marine State Park, 2. São Pedro and São Paulo Archipelago Natural Monument and Environmental Protected Area, 3. Fernando de Noronha National Park and Environmental Protected Area, 4. Rocas Atoll Biological Reserve, 5. Recifes de Corais Environmental Protected Area, 6. Costa dos Corais Environmental Protected Area, 7. Baía de Todos os Santos Environmental Protected Area, 8. Abrolhos Marine National Park, 9. Trindade and Martim Vaz e do Monte Columbia Natural Monument and Trindade and Martim Vaz Archipelago Environmental Protected Area, 10. Costa das Algas Environmental Protected Area, 11. Arraial do Cabo Marine Extractive Reserve, 12. Tamoios Ecological Station, 13. Litoral Norte São Paulo Marine Environmental Protected Area, 14. Area of Relevant Ecological Interest Queimada Pequena and Queimada Grande Islands, 15. Arvoredo Marine Biological Reserve, 16. Lobos Island Wildlife Refuge.

3.3. Latitudinal Patterns of Taxonomic Distinctness

The taxonomic distinctness average ($\Delta+$) along a latitudinal gradient differed among taxonomic groups (Figure 6). For Ochrophyta, $\Delta+$ was inversely related ($p < 0.05$) to latitude, while for Rhodophyta and Chlorophyta, $\Delta+$ values remained constant across latitudes (Figure 6). On the other hand, $\Delta+$ showed no relationship with latitude; however, Chlorophyta and Ochrophyta had higher $\Delta+$ values than Rhodophyta (Figure 6).

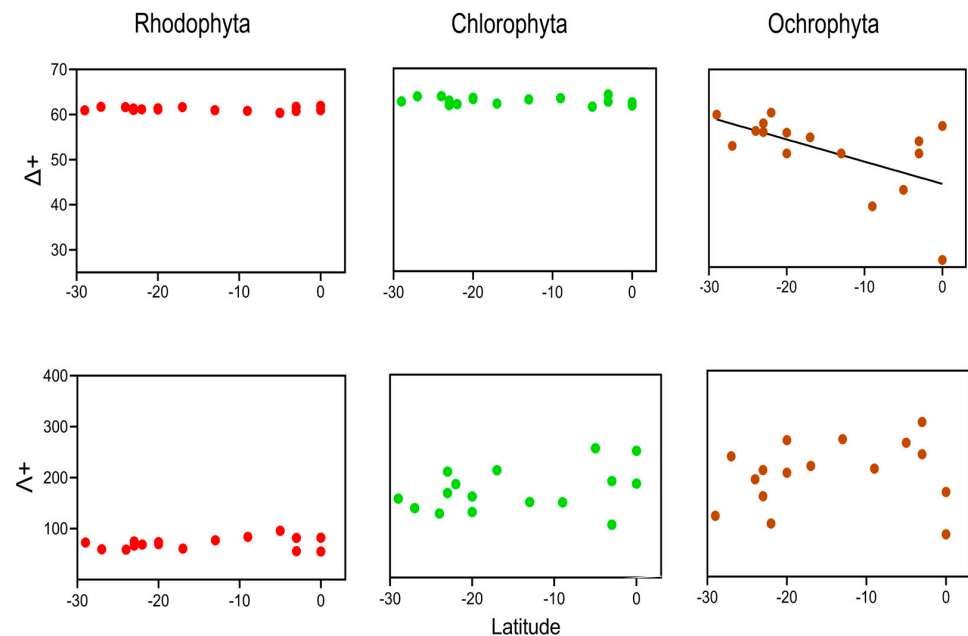


Figure 6. Average ($\Delta+$) and variation ($\Lambda+$) in taxonomic distinctness of Rhodophyta (red), Chlorophyta (green) and Ochrophyta (brown) assemblages across Marine Protected Areas (MPAs) along the latitudinal gradient (0–29° S) in the Southwest Atlantic (SWA). The line represents the linear regression.

4. Discussion

The 16 MPAs inventoried harbor 695 species distributed across eight ecoregions along a clear latitudinal gradient. Species richness exhibited a mid-latitude peak and declined toward both the northern and the southern ends of the Brazilian coast. Latitudinal variation in species composition was mainly driven by turnover, indicating a continuous replacement of species. This pattern corroborates previous findings from multi-taxa analyses on the South Atlantic rocky shores [17], which showed that the latitudinal variation in species composition is driven by turnover, rather than nestedness.

4.1. Species Richness of MPAs

The first recorded 504 Brazilian macroalgal species [15] (65% Rhodophyta, 22% Chlorophyta and 13% Ochrophyta) were distributed across four phycogeographical zones: (1) Northern/Equatorial: low diversity; (2) Western/Northeastern: highest diversity; (3) Southeastern: well-developed flora supported by rocky shores; and (4) Southern: decreasing species richness. Later, Ref. [16] reported 642 infrageneric taxa along the coast of Brazil, distributed into two regions, a tropical and a warm-temperate, separated by a transition zone that corresponded to the highest richness on the Espírito Santo state coast. Since then, numerous macroalgal inventories have been carried out (Supplementary Material S2—List S1).

In this study, MPA species richness followed a latitude pattern, peaking at mid-latitudes (13–22° S) and declining toward the northern (0° S) and southern ends (29° S). This mid-latitude region likely functions as an ecotone, characterized by great diversity

and heterogeneity of habitats, which support elevated species richness [52]. Moreover, sea surface temperatures (SST) in this region facilitate the overlap of typically tropical and subtropical taxa, driven by the intrusion of the cooler South Atlantic Central Water (SACW, $<20^{\circ}\text{C}$) during the upwelling in Cabo Frio 22°S ; [53]. The region extending from Bahia to the northern part of Rio de Janeiro state has also been reported as a hotspot of coralline red algae [54], and as the region with the highest richness of benthic organisms and reef fishes across the Brazilian coast $\sim 18\text{--}22^{\circ}\text{S}$; [19,55,56], this reinforces its role as a transition zone.

The reduction species richness at the Parcel de Manuel Luís MPA (46 species), in the Amazonia ecoregion, and at Lobos Island MPA (64 species), in the Rio Grande ecoregion, reflects the influence of two larger estuaries, the Amazon River and the Patos Lagoon, respectively [53]. In the Amazon reef system, macroalgal distribution is strongly influenced by the Amazon River plume, with diversity increasing southwards toward the offshore coral reefs at the Parcel de Manuel Luís MPA [57]. A reduced plume influx favors a higher coralline algae diversity and dominance of fleshy macroalgae in southern part of the Amazon reef system, i.e., the Parcel de Manuel Luís MPA [19,57]. In the southernmost region of Brazil, large fluvial inputs from the La Plata River and the Patos-Mirim Lagoon, together with the complex thermohaline associated with two water masses, influence the macroalgal distribution in this region [58]. These two MPAs have also been less surveyed than the other MPAs, suggesting that their species richness may be underestimated.

Species richness recorded in the 16 MPAs (695 species) and endemism (26 species) are high compared with those of Brazilian flora; however, they are likely still underestimated. Some groups, such as turf-forming algae and epiphytic species, are rarely identified at the species level due to their small size and difficulty of identification. Calcareous algae, including NGCA, brown crusts and Peyssonneliales, are also likely underestimated in the SWA, as many records are based on morphological taxonomy. Despite recent progress in molecular approaches, many NGCA taxa are still not defined [59], and the high NGCA endemism in rhodolith beds and rocky shores suggests that much of their biodiversity remains unknown.

4.2. Latitudinal Patterns of Species Composition

Macroalgal species composition across the studied MPAs was distributed continuously along a broad latitudinal range, from Fernando de Noronha (3°S) to São Paulo Litoral Norte (23°S), through the northeastern, eastern and part of southeastern Brazil ecoregions. The region between 5°S and 20.5°S is strongly influenced by the Brazil Current (BC; [60]), a western current originating from the bifurcation of the southern branch of the South Equatorial Current (SEC; 10°S) and flowing southward to the Subtropical Convergence Zone (SCZ; 38°S) [61]. The BC is associated with two water masses: Tropical Water (TW) ($>20^{\circ}\text{C}$), and the SACW ($6\text{--}20^{\circ}\text{C}$). In the southeastern Brazil ecoregion, the Arraial do Cabo, Tamoios and São Paulo Litoral Norte MPAs ($22\text{--}23^{\circ}\text{S}$) harbored similar macroalgal assemblages under the influence of SACW upwelling, which extends southward to Santa Marta Cap, in Santa Catarina state. This region acts more as a genetic filter rather than a barrier for most benthic marine organisms [59]. Upwelling conditions favor macroalgal species with a high affinity for cooler waters at tropical latitudes [62]. Farther south, Santa Catarina state, where Arvoredo MPA is located about 200 km from the coast, harbors 40–50% tropical species and 30% subtropical species [58]. Although Ref. [58] reported high floristic similarity between Santa Catarina state and Torres (1.8 km from Lobos Island), our results show that species composition in Arvoredo MPA differs markedly from that of Lobos Island MPA. These MPAs feature distinct environmental conditions and habitats. The flora of Arvoredo MPA is highly diverse, due to the presence of extensive rhodolith beds, the southernmost formations on the SWA shelf [63]. The Ilha dos Lobos MPA is a

geologic relict, comprising a mosaic of consolidated substrates that provide microhabitats where macroalgae, particularly coralline algae, thrive [64].

Rhodophyta assemblages from Abrolhos MPA were more similar to those from the oceanic islands and distinct from those of the eastern Brazil ecoregion, likely due to its offshore location. Across the northeastern, eastern and southeastern Brazil ecoregions, MPAs showed similarity over a broader latitudinal range (5–27° S; Figure 4), compared to the overall flora, and included two southern MPAs, Queimada Grande and Arvoredo. The discontinuity among these southern areas when analyzing overall flora resulted from high dissimilarity in both Chlorophyta and Ochrophyta. Ochrophyta, in particular, showed greater overall heterogeneity in community composition across latitude, with rocky shore MPAs being distinct even among nearby areas, as Arraial do Cabowhich had the highest species richness for this group (40 species, Table 2). Considering the dissimilarity in species composition across the latitudinal gradient, the most distinct areas were the Parcel de Manuel Luís and the São Paulo and São Pedro MPAs. Effective conservation of macroalgal diversity should not rely solely on the most species-rich sites but also consider these unique assemblages.

In our study, changes in species composition among MPAs were mostly driven by spatial turnover (88%) rather than nestedness (4%), indicating continuous species replacement rather than loss or gain across the latitudinal gradient, consistent with South Atlantic multi-taxa patterns [17]. In the SWA, β -diversity is strongly influenced by SST gradients, with some transition zones [16,65]. SST gradients and primary productivity hotspots, such as upwelling and convergence zones, drive variation in macroalgal assemblages and may exert major influence on large-scale evolutionary and historical processes [17].

β -diversity partitioning remains rarely employed in phycological studies [48]. Floristic studies have shown that environmental changes in areas of high turnover are expected to result in significant biotic responses [66]. In the ocean, temperature seems to be the main large-scale latitudinal driver for high turnover rates [67], while other drivers, such as nutrients, salinity, turbidity, wave action and photoperiod may also influence species composition, depending on the regional context. In South Africa, two different macroalgal community structuring systems were reported: in the Atlantic Ocean, a thermal gradient driven by the Agulhas Current explained most of turnover variation, suggesting that niche-driven processes are dominant; in the Indian Ocean, a weaker thermal gradient led to higher nestedness [48].

4.3. Latitudinal Patterns of Taxonomic Distinctness

Latitudinal patterns in species composition are influenced by three non-exclusive factors: ecological, evolutionary and historical processes [50]. In our results, $\Delta+$ increased with latitude for Ochrophyta, while $\Delta+$ for Rhodophyta and Chlorophyta showed no latitudinal variation. The observed patterns, a mid-latitude peak in species richness, high species turnover, and constant taxonomic distinctiveness, suggest that changes across the latitudinal gradient are primarily driven by ecological processes. In contrast, brown algae showed higher $\Delta+$ towards the warm-temperate zone, consistent with global and regional diversity patterns for this group [17,68,69]. The higher degree of diversification observed in brown algae towards the south may result from the interplay between evolutionary processes, which drive lineage diversification, and ecological factors, which promote species replacement along an environment gradient.

In the Brazilian Province, isolations of the northeastern and southeastern phylogroups have been reported due to historical processes, including Holocene sea-level fluctuations [70,71], and the emergence of the Vitória-Trindade seamount chain (19–21° S) during periods of glacial maxima [72].

4.4. Implications to Conservation and Management

Along the SWA (0–27° S), benthic communities on biogenic and rocky reefs are dominated by turf algae ($52.9\% \pm 27.6$ SD) and fleshy macroalgae ($17.36\% \pm 24.04$ SD) [19]. Turf algae dominate both biogenic reefs and coastal rocky shores, while macroalgae are more abundant in offshore areas [19,22]. Our results indicate that the studied MPAs may support high diversity; however, in areas with increased turbidity and SST, turf-macroalgal dynamics dominate reef benthic communities and may reduce diversity. Turf algae are strongly associated with turbid waters in positive ecological feedback that reduces herbivory by fish [73]. Addressing these factors through conservation and management actions will be essential to enhance marine biodiversity conservation and ecosystem resilience.

Our results highlight the importance of ensuring effective protection of these MPAs, which are repositories of high species richness and heterogeneity. Furthermore, the MPAs with the highest macroalgal species richness, Baía de Todos os Santos, Arraial do Cabo, and Costa das Algas, are multiple-use areas that encompass several ecosystems, such as biogenic reefs, rocky shores and rhodolith beds. However, high diversity within these areas does not necessarily translate into effective protection of the greater biodiversity, unless macroalgal communities are fully incorporated into conservation and management plans. Therefore, management actions need to be strengthened to address global and local pressures, mainly in coastal multiple-use areas. These findings emphasize the need to expand the no-take areas in high biodiversity habitats to ensure that they are effectively safeguarded and integrated with multiple-use areas.

Understanding the processes influencing species turnover and geographical ranges is essential for effective spatial biodiversity planning. Focusing conservation and monitoring efforts on areas of high species turnover will help preserve both species diversity and their environmental niches [48].

In addition, current MPAs do not adequately protect representative macroalgal habitats or endemic species, and mid- and offshore habitats remain largely outside the national network of protected areas. A case in point is the endemic mesophotic kelp *L. abyssalis*, which forms deep-water beds on rhodolith substrates at depths between ~40 and 120 m between latitudes 19–23° S under low-light conditions and the influence of upwelled SACW [74]). Consequently, these kelp–rhodolith systems, critical for the persistence of *L. abyssalis*, remain poorly covered by no-take areas and are vulnerable to disturbance.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/d18010001/s1>. Supplementary Material S1: Table S1: Main habitat, ecoregion, surface area and coordinates of Marine Protected Areas (MPAs). Ecoregion according to [14]; Area of polygons calculated using Geographic Information System—GIS (Cadastro Nacional de Unidades de Conservação); Table S2: Old and updated nomenclature of Brazilian macroalgae (2025); Table S3: Compiled list of marine macroalgae of sixteen Marine Protected Areas (MPAs; List of MPAs in Table S1). Supplementary Material S2: List S1: References of data obtained for each Marine Protected Area (MPA); List S2: Checklists of marine macroalgae published in the Catálogo de Plantas das Unidades de Conservação do Brasil

Author Contributions: Conceptualization: C.S.K., V.C., J.M.d.C.N., M.T.F., F.C.d.M. and L.T.S.; data compilation: C.S.K., C.C.d.S., P.S.M. and A.V.C.d.O.; data organization: C.C.d.S., J.M.d.C.N., G.d.N.S., V.C., M.T.F., F.T.d.S.T., P.S.M. and A.V.C.d.O.; list validation: G.d.N.S., V.C., M.T.F. and J.M.d.C.N.; data analyses: E.G.-C. and C.S.K.; publication of lists: L.T.S. and C.S.K.; writing: C.S.K., E.G.-C., C.F.D.G. and R.d.G.B.; manuscript revision: C.S.K., E.G.-C., V.C., C.F.D.G., R.d.G.B., R.T.d.C., F.T.d.S.T., M.T.F. and J.M.d.C.N.; editing: C.S.K., E.G.-C., C.F.D.G., R.d.G.B., R.T.d.C. and M.T.F. All authors have read and agreed to the published version of the manuscript.

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