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Brazilian Coast: A Significant Gap in the Knowledge of Cyanobacteria and Their Applications

Taiara A. Caires and Helen Michelle de J. Affe

Abstract

Brazil has 10.959 km of coastline which includes three ecoregions based on the biogeographic system, exhibiting a wide range of environments that favor the occurrence of numerous cyanobacterial morpho- and ecotypes. These organisms have a great adaptive capacity, which explains their occupancy in numerous environments and the high diversification of the group. Historically, the cyanobacteria have been classified only based on morphology, which makes their taxonomy quite challenging. There is usually little morphological variation between taxa, which makes it difficult to identify diacritical characteristics between some genera and species, making intergeneric and intraspecific delimitation tough. Thereby, the polyphasic approach based on different tools allows the identification of new taxa and the reassessment of those already established with more reliability, contributing to a better systematic resolution of the world 'cyanoflora', a term that we propose herein to describe the diversity of Cyanobacteria into Phycoflora area. However, the use of these tools is still not widely applied to most genera and species, especially those from tropical and subtropical environments, which has limited the real recognition of their biodiversity, as well as the knowledge about the cyanobacteria's evolutionary history and biogeography. In Brazil, even with the great development of phycological studies, the knowledge about Cyanobacteria from marine benthic environments has not evolved to the same degree. This phylum has been neglected in floristic surveys, presenting only 46 benthic species reported to the long Brazilian coastline, evidencing the still incipient knowledge about the diversity and distribution of this microorganism's group. Furthermore, biotechnological properties of Brazilian marine cyanobacteria are still almost completely unknown, with only three studies carried out to date, underestimating one of the most diverse groups and with promising potential for the possibility of isolating new biochemically active compounds. The ten new taxa related to the Brazilian coast in the last decade emphasizes the challenge of conducting further floristic surveys in the underexplored marine environments in order to fill an important lacune in the cyanoflora knowledge, as well as their biogeographic distribution and biotechnological potential. Besides, the recognition of the Brazilian cyanoflora makes an important contribution to the understanding of the functioning and monitoring of marine ecosystems and provide data for the construction of future public policies, which is a goal of the United Nations Decade for Ocean Science for Sustainable Development.

Keywords: biodiversity, biotechnological prospection, Brazilian coast, cyanoflora, cyanobacteria, polyphasic approach, taxonomy

1. Introduction

The phylum Cyanobacteria is a well-defined group of gram-negative oxygenic photosynthetic bacteria, responsible for the initial change of the Earth's atmosphere from the reducing to the oxidizing condition [1–4]. The origin of this group is estimated between 2.7 to 3.5 billion years, based on fossil records and organic biomarkers. Cyanobacteria are highly adaptable and have colonized the most varied biotopes as terrestrial, freshwater, brackish, and marine environments, including those considered extreme, such as the poles, hot springs, and deserts, being considered excellent environmental colonizers [5–7].

The adaptive capacity and diversification of cyanobacteria, as well as the occupation of the environments by these microorganisms can be explained by their great flexibility to acclimatize to a wide range of environmental conditions [1, 4, 8]. This extraordinary adaptability is favored by a wide variety of morphological and physiological characteristics exhibited by different eco- and morphotypes into Cyanobacteria [7]. Besides their significant ecological importance as primary producers, these organisms also are recognized as great fixers of atmospheric nitrogen, playing an important role in the bioavailability of the nitrogen compounds in the trophic chains of the most diverse environments, whether aquatic or terrestrial [9].

Cyanobacteria usually present phenotypic plasticity among the individuals of the same species. On the other hand, individuals from different species can represent cryptic taxa [10]. For marine environments, these morphological variations may be due to local environmental features, such as hydrodynamics, water temperature, shading, and substrate types [11]. According to Dvořák et al. [12], the difficulty of cyanobacteria identification stems from their cryptic diversity, as well as the poor knowledge about morphological variability of these organisms and the common convergent evolutionary events. Thus, the polymorphism presented by cyanobacteria makes it difficult to identify diacritical characteristics for species identification [11, 13].

Historically, the cyanobacteria have been classified only based on morphology, which makes their taxonomy quite challenging, especially on intergeneric and intraspecific delimitation. In that respect, the polyphasic approach has been widely used in taxonomic studies of cyanobacteria as an efficient method to identify new taxa and reassessing of those already established [4, 14]. This approach mainly integrates molecular data (e.g. 16S rRNA), morphology, ultrastructure, biochemistry and ecological aspects. The recent inclusion of new molecular biology tools has been particularly useful, as the secondary structure of the internal transcribed spacer (ITS) located between the 16S and 23S rRNA genes [15–18].

The integration of these tools has helped in the resolution of countless cryptogenera, which present distinct phylogenetically well-defined clades, but practically impossible to be separated only by morphology [4], clearly showing that genotypic diversity exceeds phenotypic diversity. Thereby, the polyphasic approach allows greater knowledge about polyphyletic genera [10, 19–26], contributing to a better systematic resolution of the world 'cyanoflora', a term that we propose herein to describe the diversity of Cyanobacteria into Phycoflora area.

However, the use of these tools is still not widely applied to most genera and species, especially those from tropical and subtropical environments, which has limited the real recognition of their biodiversity, as well as the knowledge about the cyanobacteria's evolutionary history and biogeography. This group has been neglected in the Brazilian marine floristic surveys, mainly for benthic environments, which are still poorly understood. Besides the difficulties in carrying out taxonomic studies due to the great problem in the definition of

diacritic characteristics that assist in rapid and practical identification of taxa [27], it is important to highlight the small number of taxonomists working in this specific group in Brazil, which amplifies the significant knowledge gap about the cyanoflora.

2. Brazil: an extensive and environmentally diverse coastline

Brazil has 10.959 km of coastline (4°N to 33°S) which is bathed in its entire length by the Atlantic Ocean. Additionally, its coast has an Exclusive Economic Zone (EEZ) that includes up to 200 miles from the coast, encompassing the entire Continental Shelf and the oceanic islands [28]. The Brazilian coast is subdivided into three ecoregions based on the biogeographic system to classify the oceans: (1) Warm Temperate Southwestern Atlantic (South and Southeast regions); (2) Tropical Southwestern Atlantic (East and Northeast regions); and (3) North Brazil Shelf (Amazonia region) [29]. Included into the Tropical Southwestern Atlantic ecoregion are São Pedro & São Paulo Islands, Fernando de Noronha, Atoll das Rocas, Trindade and Martin Vaz Islands, and the Abrolhos Archipelago (**Figure 1**).

Horta et al. [30], based on the latitudinal temperature gradient occurring along the Brazilian coast, divided it into two large areas: (1) Tropical Region (covering the Northeast area); and (2) Warm Temperate Region (including the Southeast and South areas, with exception of Espírito Santo state, which is considered a transition zone) (**Figure 1**). The Tropical Region is characterized by the oligotrophic waters and its benthic phycoflora is found predominantly on sandy substrates. In the Warm Temperate Region, the benthic algae occur on rocky shores [30–32].

For macroalgae, the species richness presents a reduction in the north–south direction along the Brazilian coast [30]. The obtained data so far show this same pattern of species richness distribution for cyanobacteria. However, there are many

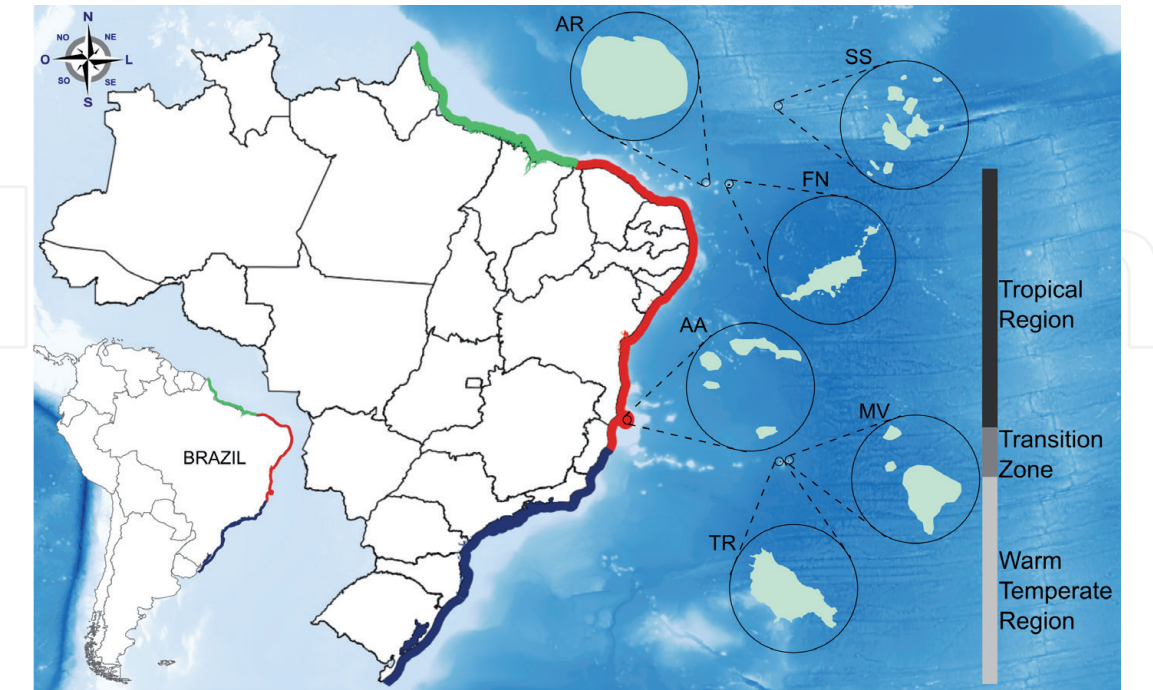


Figure 1. Ecoregions (colored lines) based on Spalding et al. [29], and regions (gray scale bars) based on Horta et al. [30]. Green - North Brazil shelf; red - tropical southwestern Atlantic; blue - warm temperate southwestern Atlantic. AR - Atoll das Rocas; SS - São Pedro & São Paulo Islands; FN - Fernando de Noronha; TR - Trindade Island; MV - Martin Vaz Islands; AA - Abrolhos archipelago.

knowledge gaps about this group in the Brazilian coastline, which can modify this pattern observed up to now. Golubic et al. [33] and Hoffmann [34] highlighted that large areas with different climates can present a high cyanobacteria biodiversity, notably in the tropical zone, in which the great part of the Brazilian coast is found.

The Brazilian coastal region varies considerably in shape and width, including 3.000 km of coral reefs (0°50'S to 18°00'S) among which some are attached to the coast, and others are several kilometers offshore [35–37]. Charpy et al. [38] relate that benthic cyanobacteria constitute a major component of epiphytic, epilithic, and endolithic communities in reef ecosystems, performing an important role in these areas. Besides the coral reefs, the Brazilian coast presents several types of substrates, including beach rocky, sandstone formation, precambrian basement, and carbonate crusts, which can favor the occurrence of a great diversity of cyanobacteria (**Figure 2**).

In the marine benthic environments, the cyanobacteria can occupy the supralittoral, mediolittoral (intertidal zone) and infralittoral, which may grow in epilithic, epiphytic, and epizotic life forms [11, 39–41]. Cyanobacteria do not have specific morphological adaptations for fixation. Thus, these organisms typically occur associated with rough substrates, as beach rock which favors their adhesion, and microhabitats which present low hydrodynamics [41]. According to Taton and Hoffmann [42], these microorganisms can occur as endoliths in the locals with high water movement.

Regarding the vertical zonation in these environments, the morphophysiological characteristics of cyanobacteria play an important role in their distribution. Taton and Hoffmann [42] describe that these microorganisms can display zonation from supralittoral areas toward the intertidal zone, which is directly influenced by hydrodynamics, duration and frequency of subaerial exposure, and the type and amount

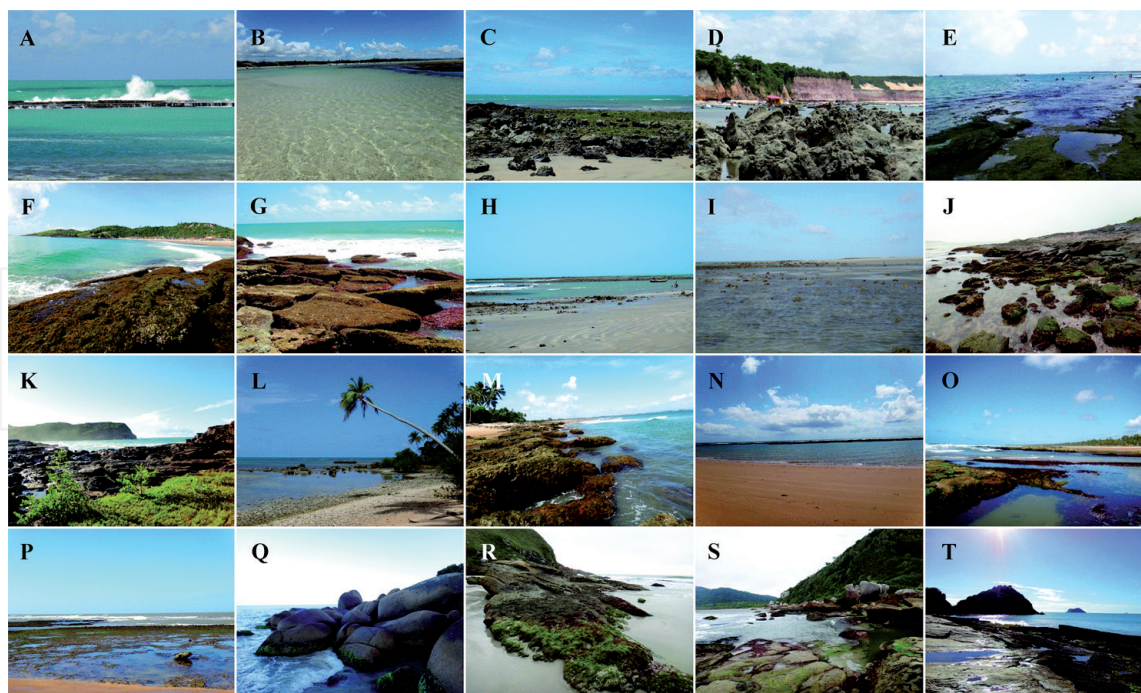


Figure 2.

General aspect of beaches on the Brazilian coast. **A.** Praia do Francês (TSA); **B.** Paripueira (TSA); **C.** Pirambúzios (TSA); **D.** Pipa (TSA); **E.** Porto de Galinhas (TSA); **F.** Gaibú (TSA); **G.** Caponga (TSA); **H.** Itaquí (TSA); **I.** Araçagi (NBS); **J.** Pontal de Guaibura (WTSA); **K.** Praia das Focas (WTSA); **L.** Praia de Tassimirim (TSA); **M.** Ponta do Mutá (TSA); **N.** Praia do Francês (TSA); **O.** Imbassaí (TSA); **P.** Praia dos Castelhanos (WTSA); **Q.** Ponta das Canas (WTSA); **R.** Ponta da Nhá Pina (WTSA); **S.** Praia Grande (WTSA); **T.** Búzios (WTSA). (WTSA) Warm Temperate Southwestern Atlantic ecoregion (south and southeast regions); (TSA) Tropical Southwestern Atlantic ecoregion (east and northeast regions); (NBS) North Brazil Shelf ecoregion (subregion Amazonia region).

of sediments. In that respect, the presence of heterocytes can favor the survival of these microorganisms in microhabitats with limited nutrient availability, as the supralittoral. Tomitani et al. [43] and Sohm et al. [44] related the predominance of Nostocales taxa in this abovementioned microhabitat, which has limiting abiotic variables.

On the other hand, homocyted taxa present high success in several microhabitats in the mediolittoral region, which remain in contact with water for a period of the day [41]. Besides the aforementioned zones, the infralittoral region is also understudied in the Brazilian marine environments, with only one species described for this zone, *Symploca infralittoralis*, Caires et al. [40], highlighting the need for greater sampling and analysis efforts in this environment.

3. How much is Brazilian marine benthic cyanoflora known?

In Brazil, even with the great development of phycological studies, the knowledge about the phylum Cyanobacteria has not evolved to the same degree, especially regarding the marine benthic environments [41, 45]. According to Komárek [46], only 5 to 10% of the diversity of cyanobacteria is known in the world. Menezes et al. [47] carried out a data compilation and registered the following species richness for the Brazilian marine environments: North - one taxon; Northeast - 45 taxa; Southeast - 91 taxa; and South - 16 taxa. However, these numbers include the diversity of planktonic cyanobacteria, which are more widely known than benthic ones.

Regarding the benthic taxa for the Brazilian coastal region, only 46 species are reported by 'Flora do Brasil 2020 Database', which are distributed as follows: 25 species for Oscillatoriales (homocyted taxa); six species for Nostocales (heterocystous taxa); two for Spirulinales (homocyted taxa); seven for Synechococcales (five homocyted taxa; and two single-celled taxa); four species for Chroococcales (single-celled taxa); and two species for Pleurocapsales (single-celled taxa) [48].

Cyanobacteria is a group of great ecological, health, economic and biotechnological interest nevertheless studies approaching benthic marine cyanobacteria in Brazil are scarce (**Figure 3**). Among the realized studies, most of them were developed in the southeastern region, mainly in the coastal environments of the São Paulo and Rio de Janeiro states, both included in Warm Temperate Region [49–65].

For the other Brazil's regions, the following studies are reported: South – Coutinho et al. [66] for Santa Catarina state, and Garcia-Baptista & Baptista [67] for Rio Grande do Sul state; and Northeast – Nogueira and Ferreira-Correia [68] for Maranhão, Branco et al. [69] for Pernambuco, and Caires et al. [10, 40, 41] for Bahia. Additionally, Caires et al. [70] described one new genus, *Neolynghya* T.A. Caires, C.L. Sant'Anna et J.M.C. Nunes, which includes six species widespread for the Brazilian coast. Among them, *N. granulosa* T.A. Caires, C.L. Sant'Anna et J.M.C. Nunes was recently reevaluated based on genetic data by Lefler et al. [26], who proposed a new combination *Affixifilum granulosum* (Caires, Sant'Anna et Nunes) Lefler, D.E. Berthold et Laughinghouse.

Besides *Neolynghya*, other two new genera were described for Brazilian coast in the last decade: *Capilliphycus* T.A. Caires, C.L. Sant'Anna et J.M.C. Nunes [10], including two species (*C. salinus* T.A. Caires, C.L. Sant'Anna et J.M.C. Nunes, and *C. tropicalis* T.A. Caires, C.L. Sant'Anna et J.M.C. Nunes); and *Halotia* D.B. Genuário et al., with one species for marine benthic environment (*H. branconii* D.B. Genuário et al.). The distribution of the ten new species, including *Symploca infralittoralis* described for the Brazilian infralittoral, is showed in **Figure 4**.

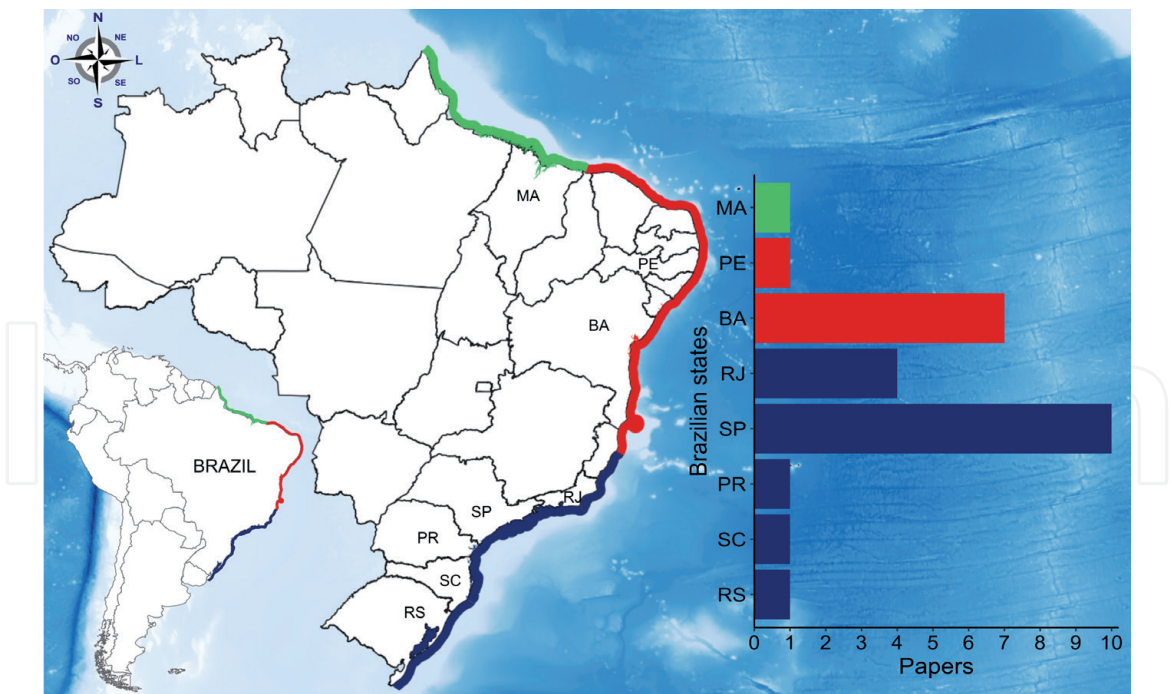


Figure 3. Number of papers about benthic cyanobacteria developed in each coastal region Brazilian coastline: Green - North Brazil shelf (one study); red - tropical southwestern Atlantic (eight studies); blue - warm temperate southwestern Atlantic (seventeen studies). Brazilian states: MA – Maranhão; PE – Pernambuco; BA – Bahia; RJ – Rio de Janeiro; SP – São Paulo; PR – Paraná; SC – Santa Catarina; RS – Rio Grande do Sul.

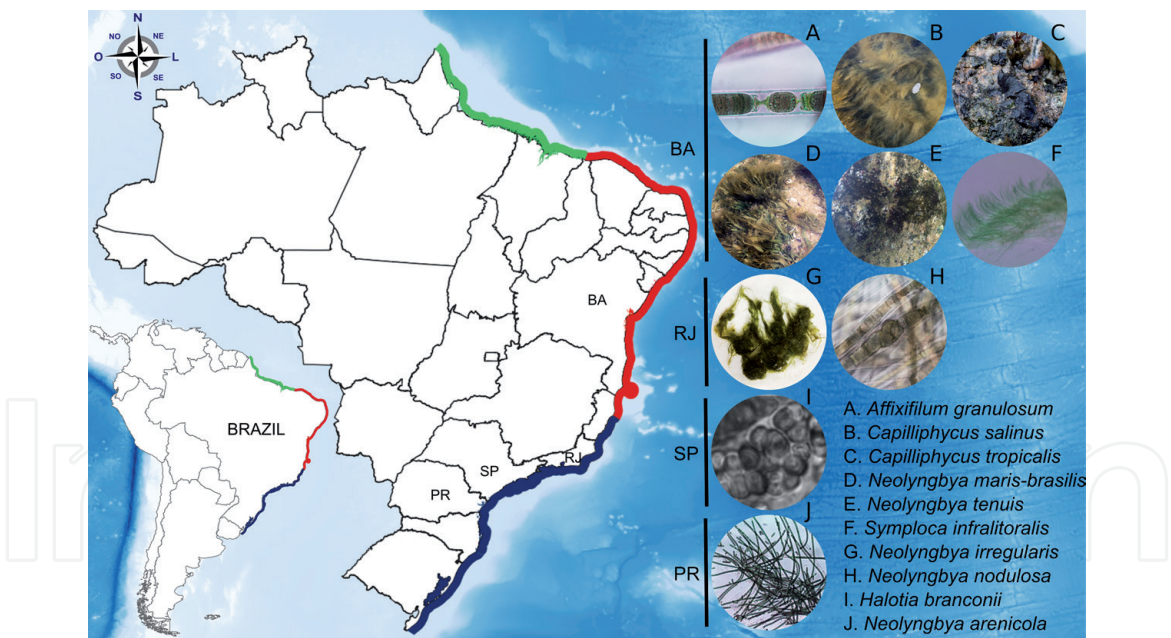


Figure 4. Spatial distribution along the Brazilian coast of the new described genera and species in the last decade. Data based on Caires et al. [10, 40, 70] and Genuário et al. [64]. Green - North Brazil shelf (no taxon); red - tropical southwestern Atlantic (six taxa); blue - warm temperate southwestern Atlantic (four taxa). Brazilian states: BA – Bahia; RJ – Rio de Janeiro; SP – São Paulo; PR – Paraná.

Since the first published research about Brazilian marine benthic cyanobacteria which was carried out almost four decades ago, a limited number of studies was realized in this country (**Figure 5**). The number of studies and the interval among them demonstrate that the knowledge about the diversity and distribution of cyanobacteria are still incipient, especially when considering the coastal extension of Brazil and the great diversity of favorable habitats for the development of these organisms [41].

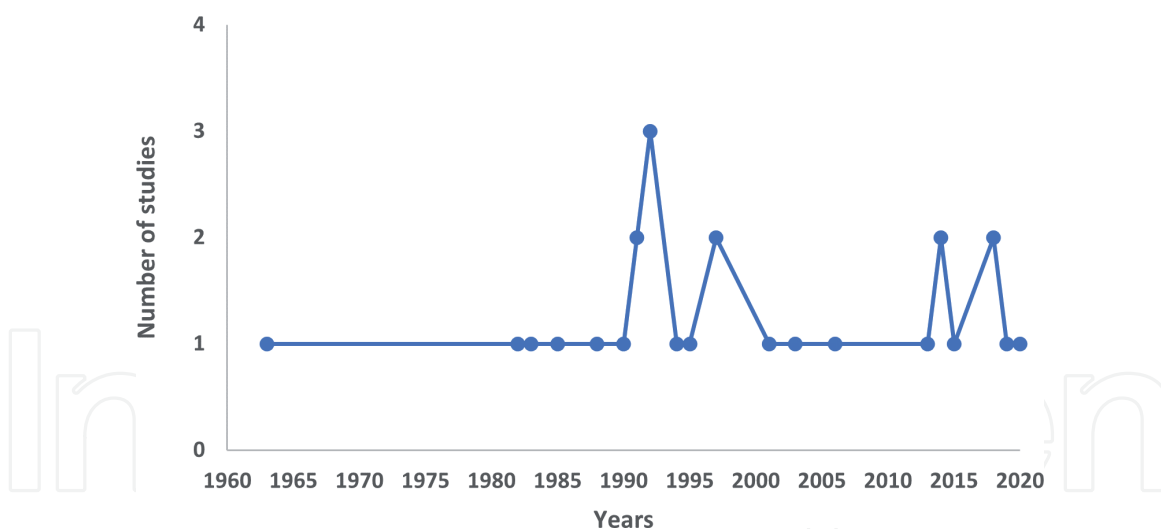


Figure 5.
 Distribution of all studies carried out about marine benthic cyanobacteria in the Brazilian environments over time.

Furthermore, Brazil has some islands, as São Pedro & São Paulo, Fernando de Noronha, Atoll das Rocas, and Trindade and Martin Vaz, which are completely unknown about their cyanoflora, underestimating the biodiversity of this group. For Abrolhos Archipelago, only the studies carried out by Walter et al. [71] and Walter et al. [72] describe a new genus, *Adonisia* Walter et al., and a new species *Adonisia turfae* Walter et al., respectively. However, the descriptions of new taxa are not valid according to the rules of the International Code of Nomenclature of Prokaryotes - ICNP [73] and the International Code of Nomenclature for Algae, Fungi and Plants - Shenzhen Code [74]. Therefore, these taxa were not included in our analyses about benthic cyanobacteria diversity.

Regarding the relevance of ecological aspects related to benthic cyanobacteria, it is important to highlight that these microorganisms also are responsible for the “Black Band Disease” in the reef-forming corals, causing a direct impact on the functioning of these systems, and affecting their entire associated biota [75]. Some filamentous species have formed recurrent blooms, as observed in Abrolhos Archipelago by Ribeiro et al. [76]. According to Taylor et al. [77], the frequency of these blooms tends to increase globally as marine ecosystems undergo a process of eutrophication and thermal anomalies, which can be associated with global climate changes. These factors make evident the importance of studies that contribute to the knowledge of cyanobacteria, as well as about the interactions between this group and other organisms that occurred in the Brazilian marine habitats, supporting initiatives for the conservation of the reef environments.

4. Underestimated biotechnological potential of the Brazilian cyanoflora

Cyanobacteria presents a great physiological ability to survive under several abiotic conditions. This capacity is possibly related to a large number of secondary metabolites biosynthesized by different biochemical routes in these individuals [78]. These compounds are distributed into 260 cyanobacterial metabolite families and in ten different chemical classes, like lipopeptides, peptides, lipids, terpenes, polysaccharides, alkaloids, polyketides, macrolides/lactones, and indole compounds, [79, 80]. Among marine cyanobacteria, the filamentous forms usually have a greater quantity of natural bioactive products, with approximately 800 compounds [81].

Therefore, these microorganisms are evaluated as a rich source of biologically active secondary metabolites with potential biotechnological application [82, 83], especially in the pharmacological area, presenting substances with antitumor, antibacterial, antiviral, antifungal, antioxidant, anti-inflammatory and anticholinesterase activities [84–102].

According to Demay et al. [80], there are more than 90 genera of cyanobacteria that produce compounds with potential beneficial activities, most of them belonging to the orders Oscillatoriales, Nostocales, Chroococcales, and Synechococcales. However, the orders Pleurocapsales, Chroococcidiopsales, and Gloeobacterales remain poorly explored about their bioactivity potential. In that respect, the marine species, specifically the complex *Lyngbya-Moorena* genera stand out for the large production of bioactive metabolites.

Although Brazil has a long coastline, showing itself as a potential source of natural products, the biotechnological properties of Brazilian marine cyanobacteria are still almost completely unknown, underestimating one of the most diverse groups with promising potential for the possibility of isolating new biochemically active compounds. In Brazil, only the studies conducted by Caires et al. [103], Vaz [62], Silva et al. [65], and Armstrong et al. [104] deal with this theme, which demonstrated the great biotechnological potential of the Brazilian marine benthic cyanobacteria, highlighting the capacity of this group.

Approaches including biofertilization and nutraceutical applications have not yet been carried out with these Brazilian marine microorganisms. For biofuel production, only the study realized by Da Rós et al. [105] with a unicellular marine strain *Chlorogloea* sp. is registered. This research evaluated the chemical and physico-chemical properties of lipids obtained from distinct cyanobacterial strains for biodiesel production.

Therefore, the extensive Brazilian coastline is almost entirely unidentified regarding the biotechnological potential of the marine cyanobacteria occurring in this environment, underestimating the biochemiodiversity of one of the most promising groups concerning the possibility of isolating new biochemically active compounds with unprecedented molecular skeletons. Thus, the use of natural compounds, as those obtained from marine cyanobacteria, has become a viable alternative for the discovery of substances for the treatment of infections caused by resistant microorganisms [106], as well as the cyanobacterial biomass can become an important source to nutraceutical, biofertilization, and biofuel applications.

5. Future perspectives about Brazilian cyanoflora

The knowledge about the biodiversity of marine benthic cyanobacteria from the Brazilian coast is notoriously underestimated. The recognition of their cyanoflora makes an important contribution to the understanding of the functioning of marine ecosystems, as well as the ecological relationships in which cyanobacteria are present, such as coral reefs. Besides, the generation of scientific knowledge about marine biodiversity is one of the goals of the United Nations Decade for Ocean Science for Sustainable Development, providing data for monitoring and conservation of these environments, in addition to the construction of future public policies [107].

The number of new taxa related to the Brazilian coast in the last decade emphasizes the challenge of conducting further floristic surveys in the underexplored marine environments in order to fill an important lacune in the cyanoflora knowledge, as well as their biogeographic distribution. The future data set based on

a polyphasic approach about this group can contribute to the definition of morphological markers for better delimitation of marine species, providing the basis for understanding evolutionary relationships and sustaining systematic decisions into Cyanobacteria. Furthermore, the recognition of this diversity supports studies that can reveal new bioactive compounds through the biotechnological prospection, aggregating value to these microorganisms.

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