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ABSTRACT

Cyanobacteria are diverse, complex and a unique group of microorganisms that inhabit a wide variety of environments. Contrarily to continental areas, studies on cyanobacteria in islands are scarce and need to be reinforced, since climate change impacts are expected to be harsher in islands, due to their geographical isolation and higher exposition to external influences. Here we present a review of the occurrence of cyanobacteria and cyanotoxins in inland and coastal ecosystems in the Atlantic Ocean islands. These microorganisms were reported from diverse habitats, including saline thermal lakes

KEY WORDS

Oceanic islands,
Iceland,
Azores,
Cuba,
biodiversity,
climate change,
CHABs.

(Iceland), freshwater lakes, terrestrial habitats (Azores, Cuba), and marine coastal areas, either planktonic (Madeira, Canary Islands, Cape Verde) or associated to plants and corals (Brazil, Caribbean Sea). Most of cyanobacteria were reported from freshwaters but some species were found in different habitats. Species richness also varied between islands, with higher number in islands located in temperate regions, and the number of common taxa was low (1-3%). Several toxic species and different types of cyanotoxins were also reported in the Atlantic islands, which are expected to increase with climate change. Mitigation measures should be considered to avoid cyanotoxins risks to environmental and public health. This work shows the great potential of Atlantic islands for cyanobacteria taxonomic, ecological and biogeography research, but more studies are needed with emphasis on less studied islands and habitats and using novel approaches as molecular systematics tools. Furthermore, such studies are of paramount importance for environmental conservation and management strategies, especially facing climate changes.

RÉSUMÉ

Un examen critique de la distribution des cyanobactéries et de la présence de cyanotoxines dans les îles de l'océan Atlantique.

Les cyanobactéries sont diverses, complexes et constituent un groupe unique de microorganismes qui vivent dans des environnements très variés. Contrairement aux zones continentales, les études sur les cyanobactéries dans les îles sont rares et doivent être renforcées, car les impacts du changement climatique risquent d'être plus sévères dans les îles, en raison de leur isolement géographique et de leur plus grande exposition aux influences extérieures. Nous présentons ici un examen de la présence de cyanobactéries et de cyanotoxines dans les écosystèmes intérieurs et côtiers des îles de l'océan Atlantique. Ces microorganismes ont été signalés dans divers habitats, notamment des lacs salins thermiques (Islande), des lacs d'eau douce, des habitats terrestres (Açores, Cuba) et des zones côtières marines, soit planctoniques (Madère, îles Canaries, Cap-Vert), soit associés à des plantes et des coraux (Brésil, mer des Caraïbes). La plupart des cyanobactéries ont été signalées dans les eaux douces, mais certaines espèces ont été trouvées dans des habitats différents. La richesse des espèces variait également entre les îles, avec un nombre plus élevé dans les îles situées dans les régions tempérées, et le nombre de taxons communs était faible (1-3%). Plusieurs espèces toxiques et différents types de cyanotoxines ont également été signalés dans les îles de l'Atlantique, dont le nombre devrait augmenter avec le changement climatique. Des mesures d'atténuation devraient être envisagées pour éviter les risques liés aux cyanotoxines pour l'environnement et la santé publique. Ces travaux montrent le grand potentiel des îles de l'Atlantique pour la recherche taxonomique, écologique et biogéographique sur les cyanobactéries, mais d'autres études sont nécessaires, en mettant l'accent sur les îles et les habitats moins étudiés et en utilisant de nouvelles approches comme outils de systématique moléculaire. En outre, ces études sont d'une importance capitale pour les stratégies de conservation et de gestion de l'environnement, en particulier face aux changements climatiques.

MOTS CLÉS

Îles océaniques,
Islande,
Açores,
Cuba,
biodiversité,
changement climatique,
CHABs.

INTRODUCTION

Cyanobacteria are ancient photosynthetic prokaryotes capable of synthesizing chlorophyll a and phycobiliproteins that were the origin of chloroplasts in eukaryotic plant cells (Whitton & Potts 2012), and played a major role in the formation of the aerobic atmosphere essential for the evolution of superior life forms (Hamilton *et al.* 2016; Codd *et al.* 2017). Formerly known as blue-green algae due to their cyan pigmentation, the size of individuals, and their ecology (Chorus & Bartram 1999), cyanobacteria are however prokaryotes with a diverse metabolism (Shevela *et al.* 2013; Codd *et al.* 2017). Besides aerobic photosynthesis, some species can do anaerobic photosynthesis (using H₂S as an electron donor), or even other metabolic pathways in the absence of light and electron donors, such as fermentation, which give them an ecological advantage (Shevela *et al.* 2013). More recently, non-photosynthetic cyanobacteria were discovered in several habitats (Soo *et al.*

2017; Monchamp *et al.* 2019), but their ecological role is still unknown (Monchamp *et al.* 2019).

Cyanobacteria have high ecological dispersion and have been reported in many environments such as aquatic (fresh, brackish, and marine waters), terrestrial (e.g. between soils and rocks), and even as aerophytic in both normal and extreme conditions (Whitton & Potts 2012; Codd *et al.* 2017; Bagchi & Singh 2019). Although present in almost all kind of habitats, cyanobacteria are more frequent in aquatic environments where they can grow suspended in water (planktic forms) or associated with substrates (benthic forms), mainly aggregated with other cyanobacteria, algae or macrophytes (epiphytic forms) (Quiblier *et al.* 2013).

Cyanobacteria specialized cells and cellular structures, such as heterocytes, akinetes, and aerotopes, are essential for their ecological advantage. Heterocytes are produced essentially in cases of nitrogen deficiency, establishing nitrogen reserves for the organism (Vincent 2009; Sarma 2012). Aerotopes



FIG. 1. — Map of the Atlantic Ocean with the location of islands with cyanobacteria references. **A**, Cuba and Bahamas; **B**, Puerto Rico, United States Virgin Islands, and Curaçao; **C**, Brazilian coastal islands - Ilha das Couves, Ilha Rapada, Ilha Anchieta, Ilha da Vitória and Ilha Bella; **D**, Brazilian coastal islands - Ilha do Cardoso and Ilha da Casca; **E**, Iceland; **F**, Azores; **G**, Madeira and Canary Islands; **H**, Cape Verde. Map sources and copyrights: Esri, HERE, DigitalGlobe, Garmin, GeoEye, Earthstar Geographics, FAO, NOAA, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, © OpenStreetMap contributors and the GIS User Community.

allow colonies to move upwards in the water column towards more favorable zones, such as zones with more incident light favoring photosynthesis (Vincent 2009). Akinetes functions vary between species, including respiratory activity, synthesis of proteins and lipids, and resistance to adverse conditions (Vincent 2009; Sarma 2012). These structures enable cyanobacteria to survive and grow under physical and chemical stress, such as extreme conditions of salinity, temperature, desiccation, or nutrient availability (Sarma 2012; Codd *et al.* 2017). Besides ecological advantage, these specialized cells are crucial for cyanobacteria taxonomic identification (Vincent 2009).

Most reports of cyanobacteria are from freshwater lakes, mainly due to massive proliferations (Cirés *et al.* 2017) essentially caused by anthropogenic influences (Paerl 2018). Cyanobacteria blooms can cause strong impacts on ecosystems biodiversity as well as in the safety of water resources for consumption if these cyanobacteria are cyanotoxin producers (Watson *et al.* 2015). In the last decades, cyanobacteria harmful blooms (cHABs) have been occurring more often (Huisman *et al.* 2018). Local anthropogenic impacts, leading to eutrophication of aquatic ecosystems, and global warming are the main reasons for the recent increase in cHABs (Paul 2008). High levels of nutrients and temperature rise (due to anthropogenic activities) are associated with the dominance of cyanobacteria either in marine or freshwater ecosystems (Paerl 2018; Mantzouki *et al.* 2018a; Huisman *et al.* 2018).

Cyanotoxins are a threat to environmental and public health, affecting the well-being of many organisms (Chorus & Bartram 1999; Watson *et al.* 2015; Huisman *et al.* 2018). The most common and well-studied are microcystin (MC) and nodularin (NOD), toxins that block protein phosphatases in

liver cells (Sarma 2012; Watson *et al.* 2015; Huisman *et al.* 2018). Other well-known cyanotoxins are saxitoxin (STX), anatoxin-a (ATX-a), homoanatoxin-a (HATX-a), and anatoxin-a(s) (ATX-a(s)), that cause the failure of normal neuromuscular communication by either paralysis or overexcitation (Sarma 2012; Watson *et al.* 2015; Huisman *et al.* 2018). Some of the less studied and reported cyanotoxins are cylindrospermopsin (CYN), aplysiatoxin (APT), lyngbyatoxin (LTX), and debromoaplysiatoxin (DTA), that cause inhibition of protein synthesis, dermatitis, and gastrointestinal inflammations (Sarma 2012; Huisman *et al.* 2018).

Unlike continental regions, studies in insular environments are scarce, hence the importance of islands cyanobacteria community's knowledge, mainly due to future alterations caused by local human impacts and climate change. This review also emphasizes the upcoming dominance of cHABs in a scenario of climate change and increasing anthropogenic pressure (Bresnan *et al.* 2013; Townhill *et al.* 2018), possibly enhanced in the more fragile insular ecosystems due to their intrinsic properties such as reduced size and isolation. Reports on cyanobacteria occurrence and cyanotoxins detection in Atlantic Ocean islands were searched in all known publications, including scientific papers, technical reports, and academic thesis.

METHOD FOR DATASET CONSTRUCTION AND ANALYSIS

Different search engines were used for the database construction, especially Web of Science and Google Scholar, without time restrictions. We searched publications that

TABLE 1. — Geographical locations and environmental characteristics of the Atlantic Ocean islands covered in this review. Air temperature (°C) and precipitation (mm) annual means were obtained from climate-data.org (<http://en.climate-data.org/>; accessed April 2020). * Brazilian coastal islands: Ilha das Couves, Ilha Rapada, Ilha Anchieta, Ilha da Vitória, Ilha Bella, Ilha do Cardoso and Ilha da Casca (air temperature and rainfall means from São Paulo state).

Islands	Latitude	Longitude	Air temperature (°C)	Precipitation (mm)
Iceland (IS)	63°9' - 66°1'N	23°1' - 14°4'W	2.9	836.6
Azores (AZ)	36°9' - 39°4'N	31°0' - 24°6'W	16.9	1028.0
Madeira (MD)	32°2' - 33°0'N	16°2' - 16°1'W	16.2	650.4
Canary Islands (IC)	27°4' - 29°0'N	13°4' - 18°0'W	20.0	137.0
Bahamas (BS)	20°9' - 26°9'N	79°3' - 73°0'W	24.9	1136.2
Cuba (CU)	20°0' - 23°2'N	84°3' - 74°2'W	25.4	1224.6
Puerto Rico (PR)	18°2' - 18°3'N	66°7' - 65°3'W	24.0	1799.5
United States Virgin Islands (VI)	17°7' - 18°3'N	64°9' - 64°7'W	26.4	1095.2
Cape Verde (CV)	14°9' - 17°2'N	25°1' - 22°9'W	24.4	181.4
Curaçau (CW)	12°1' - 12°2'N	69°0' - 68°9'W	27.3	541.0
Brazil coastal islands (BR)*	23°4' - 25°5'S	45°2' - 48°0'W	20.0	1254.4

reported cyanobacteria presence in Atlantic Ocean islands using a combination of keywords for cyanobacteria and location, such as “cyanobacteria”, “cyanotoxins”, “cyanophyta”, “blue-green algae”, and related terms, combined with “Atlantic Ocean”, “island”, “Azores”, “Bermuda”, “Canary Islands”, “Cape Verde”, “Caribbean islands”, “Faeroe Islands”, “Falkland/Malvinas Islands”, “Iceland”, “Madeira”, “São Tomé and Príncipe”, “Saint Helena, Tristan da Cunha and Ascension” or “South Georgia and South Sandwich Islands”. Reference lists of found publications were also checked for additional references.

A total of 56 publications were analyzed, from 1874 until January 2020, bringing a total of 445 cyanobacteria taxa reported from 35 Atlantic Ocean islands.

Database entries were cyanobacteria taxa identification to the lowest taxonomical level available. In case of doubtful reports, original literature or local experts were consulted. The compiled taxonomic list was checked for duplication, synonymy, and invalid taxa. Species names were revised to the most recent nomenclature according to AlgaeBase (Guiry & Guiry 2020). Each entry, or taxa, had information regarding its origin (latitude, island, archipelago, country, and Atlantic Ocean regions), habitat, method of identification, respective reference(s) and year of identification (see supplementary file Appendix 1).

The database was analyzed with resource to tools as Excel for the construction of graphs, VENNY 2.1 (Oliveros, 2007-2015) for the built of Venn diagrams and Inkscape 0.92.4 (<https://inkscape.org/pt/>) for graphs drawing and image edition. In these analysis islands were presented by absolute latitudinal order and/or grouped according to their annual mean air temperature.

CYANOBACTERIA DISTRIBUTION AND BIODIVERSITY IN THE ATLANTIC ISLANDS

ATLANTIC OCEAN ISLANDS

The present study reviews cyanobacteria records in Atlantic islands located between latitudes 64°N and 23°S and longitudes 13° and 84°W, comprehending oceanic and continental islands, with variable geological settings and climate conditions, which in turn results in a high diversity of ecosystem types (Fig. 1, Table 1).

Iceland is a North Atlantic island, near the Arctic (64° - 66°N, 14° - 23°W), highly geologically active, which makes it rich in extreme environments. For instances, sub-Arctic lakes that are fed by thermal springs, as lake Mývatn (Ersoy *et al.* 2017), have water temperature ranging from 5°C to 30°C and the Blue lagoon whose water temperature is around 40°C and with higher levels of silica and salinity (Palinska *et al.* 2018), are examples of extreme environments where bacteria, cyanobacteria, and other phytoplankton have been reported.

Extreme environments are also very common in the Azores archipelago. The nine islands that compose the archipelago are located in the Northeast Atlantic Ocean (36°-39°N, 24°-31°W) about 1300 km from Europe and 1600 km from the North American coast, above the triple junction of the North American, Eurasian and African plates. Due to this geological setting, the Azores islands are rich in aquatic habitats, including freshwater lakes (over 80; Pereira *et al.* 2014), brackish coastal lagoons, many thermal hot spots and a variety of wetland areas, that are a niche of non-studied and non-reported cyanobacteria.

Near the African coast, the scenario is different, as the volcanic archipelagos of Madeira, Canary Islands, and Cape Verde are characterized by more dry, arid and warmer conditions, which is reflected in a lower abundance of inland aquatic habitats (Ramos *et al.* 2005; Custodio & Del Carmen Cabrera 2012; Semedo-Aguiar *et al.* 2018). On the other hand, coastal and inland aquatic ecosystems are affected by the coastal upwelling and dust storms from the Sahara Desert (Caldeira *et al.* 2002; Hill *et al.* 2012; Martín-García *et al.* 2014), resulting in increased nutrient concentration that can favor cyanobacteria and algal growth. The Madeira archipelago (32°-33°N, 16°W), about 870 km from Europe and 700 km from the West African coast, is formed by two larger inhabited islands (Madeira and Porto Santo) and two groups of smaller islands that are natural reserves (Desertas and Selvagens) (Hughes *et al.* 1998; Hughes 2006; Kaufmann *et al.* 2015), with over 200 streams and 126 catchments (Marques 1994). The Canary Islands are a subtropical archipelago (27°-29°N, 13°-18°W), with seven major islands and several islets, located 100 km from Africa (Custodio & Del Carmen Cabrera 2012; Martín-García *et al.* 2014). Water in the Canary Islands is very

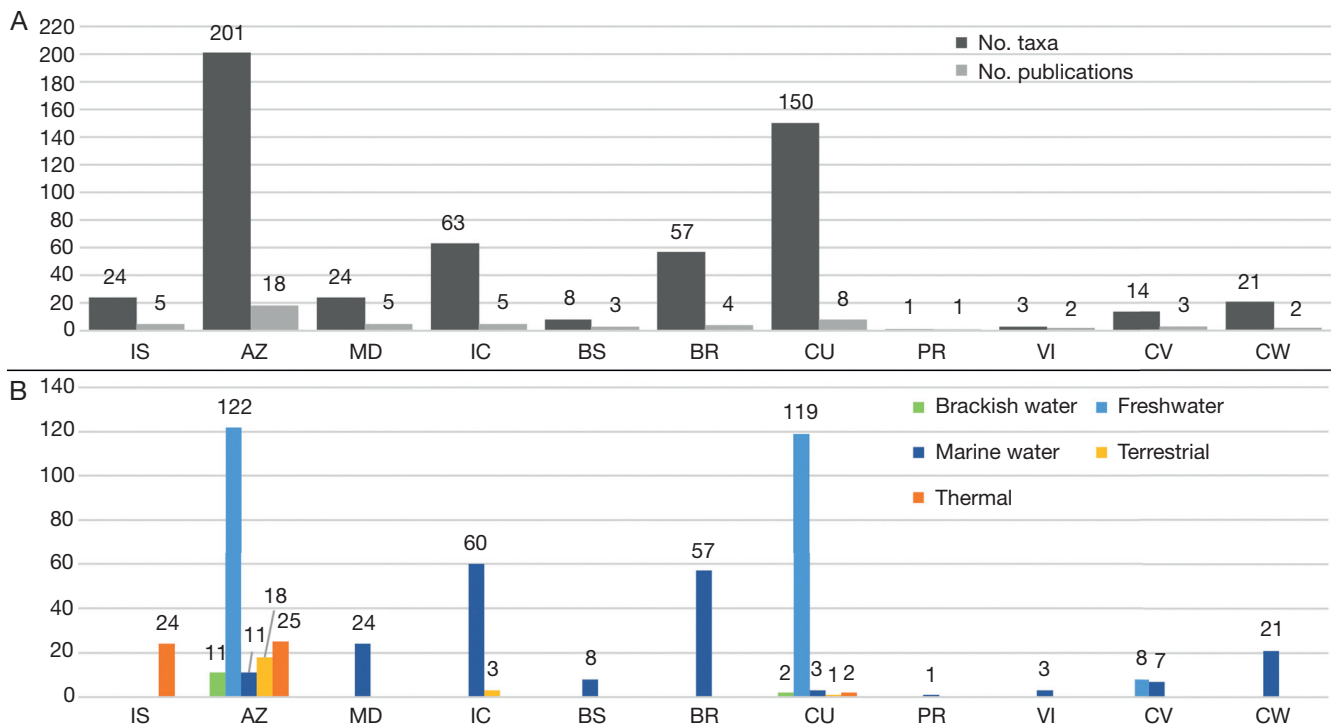


FIG. 2. — Cyanobacteria taxa distribution in Atlantic Ocean islands: **A**, total number of taxa by islands and number of publications reporting cyanobacteria; **B**, number of taxa by habitat on each island. Islands are arranged by decreasing absolute latitude. (For island codes correspondence see Table 1).

scarce, springs and streams are very few and have been drying in the last years, due to precipitation decrease and intensive groundwater exploitation (Custodio & Del Carmen Cabrera 2012). Cape Verde country is an archipelago of ten islands and 13 islets (15°–17°N, 23°–25°W), located about 455 km of the West African coast (Semedo-Aguiar *et al.* 2018). As in the Canary Islands, water is scarce in Cape Verde, due to the island's geographical location, arid environment and precipitation's instability and infrequency (Semedo-Aguiar *et al.* 2018).

Southwards, islands surrounded by warmer temperatures in the Caribbean Sea between North and South America (12°–25°N, 64°–79°W), such as the islands of Cuba, Curaçau, Bahamas, Puerto Rico, and the United States Virgin Islands, have several habitats not found in the other Atlantic islands. Most of the Caribbean Sea islands are surrounded by coral reefs with very high biodiversity (Brocke *et al.* 2015, 2018), but other ecosystems are also common among these islands such as freshwater lakes and streams (e.g. Cuba), hypersaline coastal lakes (e.g. Bahamas) and seagrasses habitats (e.g. Puerto Rico). Storr lake in San Salvador Island (Bahamas) is an example of a hypersaline coastal lake that was object of scientific expeditions and biodiversity studies (Neumann *et al.* 1988; Proença *et al.* 2009; Paul *et al.* 2016).

In the South Atlantic Ocean cyanobacteria were reported from Brazilian coastal islands (23°–25°S, 45°–48°W), mainly from marine environments (Branco *et al.* 1996; Crispino & San'Anna 2006). Brazil has a massive mangrove coastal area rich in small islands, as is the case of the Cardoso Island, from where cyanobacteria were also reported (Branco *et al.* 1996, 1997).

CYANOBACTERIA DISTRIBUTION AND BIODIVERSITY

Cyanobacteria study's in Atlantic islands are scarce however, their presence has been reported since the end of the 19th century, e.g. in the Azores archipelago (Archer 1874). The earlier records were very restricted, both in space and time coverage (e.g. Archer 1874), only the more recent studies cover a large number of habitats and longer time scales, enabling the discovery of much more cyanobacteria species (e.g. Comas 2009; Santos *et al.* 2012).

Cyanobacteria richness is uneven among islands, with the Azores presenting the highest number of reported taxa, followed by Cuba, but this result could be related to a higher sampling effort in these islands, as indicated by the higher number of published works (Fig. 2A).

A total of 445 taxa, from 129 genera and 46 families, were reported from islands in the Atlantic Ocean, between latitudes 64°N and 23°S (see supplementary file Appendix 1). Most of the reported taxa were from freshwater (226) and marine (155) habitats, 42 taxa were identified from thermal environments (Fig. 2B). As expected, most of the cyanobacteria taxa were exclusive to specific types of aquatic systems, but several were reported from more than one (Fig. 3). Twenty-two taxa (5.73%) were identified in both marine/brackish and freshwaters/terrestrial habitats, nine taxa (2.34%) were found in both freshwater/terrestrial and thermal sites, and five species were common between marine/brackish and thermal environments (Fig. 3). More surprisingly nine taxa (2.34% of total) were reported from all types of environments (Fig. 3), including six genera *Anabaena* Bory ex Bornet & Flahault, *Leptolyngbya*

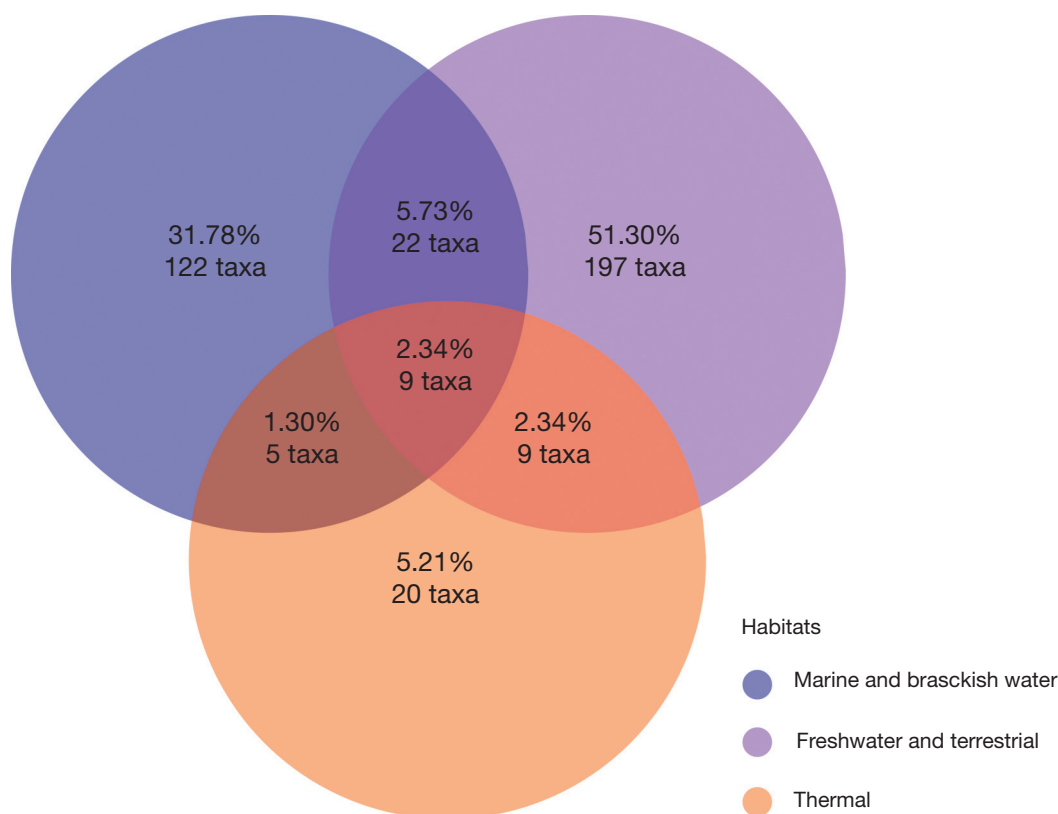


Fig. 3. — Percentage of total common and unique cyanobacteria species between three habitat groups.

Anagnostidis & Komárek, *Lyngbya* Agardh ex Gomont, *Oscillatoria* Vaucher ex Gomont, *Phormidium* Kützinger ex Gomont and *Pseudanabaena* Lauterborn, and three species *Kamptomena formosum* (Bory ex Gomont) Strunecký, Komárek & Smarda, *Lyngbya martensiana* Meneghini ex Gomont, and *Oscillatoria princeps* Vaucher ex Gomont (Appendix 1). Although some of these results could be related to incorrect identifications, they reveal the necessity of taxonomic revision of several cyanobacteria taxa as point out by Komárek *et al.* (2014).

Cyanobacteria reports from Iceland were all from thermal habitats (Fig. 2B), including common extremophile cyanobacteria species such as *Mastigocladus laminosus* Cohn ex Kirchner, *Symploca thermalis* Gomont (Castenholz 1969), and *Cyanobacterium aponinum* Moro, Rascio, LaRocca, DiBella & Andreoli (Palinska *et al.* 2018). Cyanobacteria abundance and biodiversity in Iceland's thermal habitats, when compared to other extreme environments (e.g. Yellowstone), is very low and common species in thermal habitats are absent, reinforcing the idea that geographic isolation, extremes of both cold and warmth and salt presence (saline and brackish waters) may have some forcing in species preference (Castenholz 1969; Banerjee *et al.* 2009).

In the Azores, a recent study by Luz (2018) summarizes all cyanobacteria occurrences based on morphological observations in the nine islands and different habitats published between 1874 and 2018 (Fig. 2B; Appendix 1). A total of 201 taxa were reported for the Azores, mainly from freshwaters (essentially from lakes), but also from thermal, marine and brackish habitats (Moreira *et al.* 2011; Luz 2018; Xavier *et al.* 2018; Regueiras *et al.* 2018). Species such as *Aphanizomenon flos-aquae* Ralfs

ex Bornet & Flahault, *Chroococcus turgidus* (Kützinger) Nägeli and *Oscillatoria tenuis* Agardh ex Gomont, were identified in almost all islands, in several environments such as freshwater lakes, rocks, soil or even in thermal conditions (Luz 2018).

In the Canary Islands, cyanobacteria reports are associated with marine blooms. *Trichodesmium erythraeum* Ehrenberg ex Gomont, is a threatening problem in the Canary Islands with several blooms reported since 2004 (Ramos *et al.* 2005; Arístegui *et al.* 2017). In 2017, a massive bloom of *T. erythraeum* formed in the ocean reached all islands, causing a generalized concern among local authorities and population due to its massive proliferation and MC production (Arístegui *et al.* 2017). Blooms of *Lyngbya majuscula* Harvey ex Gomont (Haroun *et al.* 2002; Martín-García *et al.* 2014) and *Aphanizomenon flos-aquae* (saxitoxin producer) (A. Martel, personal communication) have also been reported in Fuerteventura and Gran Canaria islands.

Cyanobacteria reports for Cape Verde and Madeira are scarce, probably due to a lower sampling effort in these islands (Fig. 2A). However, in the Madeira archipelago marine cyanobacteria have been reported since 1983, mainly in Porto Santo, Desertas and Selvagens islands (Weisscher 1983; Audiffred & Prud'homme van Reine 1985).

In the Caribbean islands most cyanobacteria reports are associated with black band disease (BBD), a coral disease caused by a consortium of microorganisms dominated by cyanobacteria (e.g. *Leptolyngbya*). This kind of phenomenon is very common in the Caribbean coral reefs, but also in other coral reefs around the world, as in the Great Barrier Reef

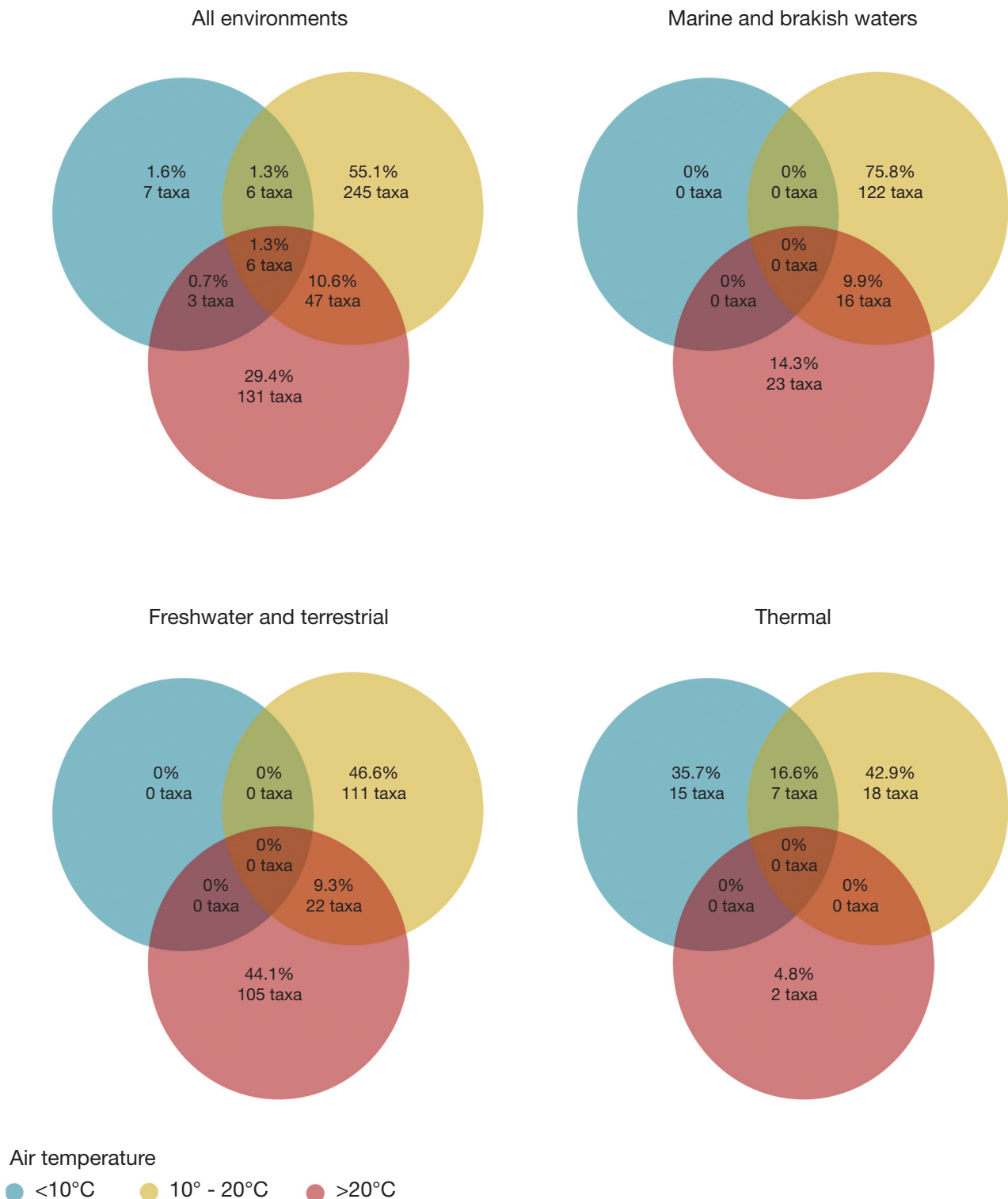


FIG. 4. — Percentage of common and unique cyanobacteria species by islands grouped according to their annual mean air temperature. “<10°C”: Iceland; “10-20°C”: Azores, Madeira, Canary Islands, and Brazilian coastal islands; “>20°C”: Bahamas, Cuba, Puerto Rico, United States Virgin Islands, Cape Verde, and Curaçau.

in Australia (Page & Willis 2006), in Indo-Pacific reefs around Palau (Sussman *et al.* 2006) and Okinawa coral reefs in Japan (Hutabarat *et al.* 2018). In Lee Stocking and Cayman Islands (Bahamas) there are reports of endosymbiotic cyanobacteria that fixate and provide corals with nitrogen (Lesser *et al.* 2007;

Olson & Lesser 2013). In Curaçau island 21 cyanobacteria taxa were identified from benthic mats associated with corals, macroalgae and substrate (Brocke *et al.* 2018). *Microcoleus lyngbyaceus* Kützinger ex Forti, was reported as an endosymbiont in seagrasses and identified as the possible cause of the decline

of this marine plant occurrence in Puerto Rico (Stielow & Ballantine 2003). In Cuba, a checklist published in 2009 (Comas 2009) reports a total of 150 taxa from different environments, such as inland brackish and freshwaters (Fig. 2B).

In South Atlantic, cyanobacteria were studied in some islands along the Brazil coast, most of them from benthic and epiphytic marine habitats (Sant'Anna *et al.* 1995; Branco *et al.* 1997; Crispino & Sant'Anna 2006). Most of the species found in these islands belonged to the orders Oscillatoriales (21), Synechococcales (13) and Chroococcales (10), which is not surprising considering the dominance of these groups of cyanobacteria in coastal mats (Stal 2000).

Total species richness does not show any evident geographical pattern (Fig. 2A), although temperate islands at mid-latitude regions present the highest overall number of taxa (Fig. 4A). Contrarily to macroorganisms, in which diversity generally decreases with latitude (Hillebrand 2004; Tittensor *et al.* 2010), global patterns of species richness were shown to present maximum values at temperate zones for marine bacteria (Ladau *et al.* 2013) and freshwater fungi (Seena *et al.* 2019). Cyanobacteria species richness in Atlantic islands seems to follow the same pattern recently found for other microorganisms, although this result needs to be interpreted with caution due to the differences in sampling effort among islands included in this review.

Despite the absence of reports on cyanobacteria from different environments in colder zones, Venn diagrams of all species and in different environments across temperature zones (Fig. 4) clearly shows that most of cyanobacteria taxa have restricted temperature ranges. Only 1.35% (six taxa) of all reported cyanobacteria are common to different temperature zones (Fig. 4A).

Most of the unique taxa were from islands located in temperate zone (annual mean air temperature between 10°C and 20°C) (254 taxa, 55.1%). Species such as *Aphanocapsa litoralis* Hansgirg, *Aphanizomenon gracile* Lemmermann, and *Chlorogloeopsis fritschii* (Mitra) Mitra & Pandey, are unique to these islands in marine/brackish, freshwaters and thermal habitats, respectively. In islands with warmer temperatures (>20°C) species as *Dichothrix utahensis* Tilden, *Woronichinia microcystoides* (Komárek) Joosten, and *Chroococcidiopsis thermalis* Geitler, are also unique in marine/brackish, freshwaters and thermal, respectively. In colder regions, in Iceland, from the 24 cyanobacteria species reported, seven were unique (e.g. *Cyanidium caldarium* (Tilden) Geitler and *Pleurocapsa minor* Hansgirg).

These results can, however, be limited by the reduced sampling effort and unequal identification methods used. Reports and observations of cyanobacteria in islands of the Atlantic Ocean, as occurs in most of other islands and countries around the world, came from earlier scientific expeditions that focused on species observation and identification as occurred in Cuba (e.g. Komárek 1995), in the Canary Islands (e.g. Afonso-Carrillo *et al.* 1983) or in the Azores (e.g. Archer 1874). More recently, publications are related to cyanobacteria isolation, culture, and genetic characterization, most of them associated with secondary metabolites identification and characterization, such as cyanotoxins. Recent reports of cyanobacteria in these islands use multiproxy approaches,

for the identification of cyanobacteria through morphological and molecular techniques (e.g. Brocke *et al.* 2018), to search secondary metabolites (e.g. Moreira *et al.* 2011; Jerez-Martel *et al.* 2017), or more focus on the ecology and distribution of toxic species (e.g. Martín-García *et al.* 2014; Mantzouki *et al.* 2018a, b). These new approaches are of major importance to unrevealing the hidden diversity in understudied environments, for example Palinska *et al.* (2018) reported three new species in Iceland by next-generation-sequencing (NGS), that were not identified previously by morphological identification. To better understand the cyanobacteria distribution in Atlantic islands larger studies with standardize sampling and identification methods are needed.

CYANOTOXINS OCCURRENCE

Cyanotoxins are toxic secondary metabolites produced by many cyanobacteria strains (Moreira *et al.* 2013; Vasconcelos 2015; Humbert & Fastner 2017), that have been more frequently reported in the past decades (Codd *et al.* 2017). Occurrence of cHABs and cyanotoxins was observed all over the world including the Atlantic islands. In the Canary Islands in 2004, MC-LR (microcystin-LR) was detected by HPLC (high-performance liquid chromatography) and immunoassay methods in a vast bloom of *T. erythraeum*, caused mainly by elevated temperatures (the highest record since 1912) and massive dust storms from the Sahara Desert (Ramos *et al.* 2005). Besides *T. erythraeum* other species described as MC producers were reported in the Canary Islands such as *Phormidium corium* Gomont ex Gomont, and *Trichormus variabilis* (Kützinger ex Bornet & Flahault) Komárek & Anagnostidis (Table 2).

In the Caribbean Sea cyanotoxins reports are mainly related to BBD associated with MC cyanobacteria producing species. Strains isolated from corals, associated with BBD, were identified as MC producers by ELISA (enzyme-linked immunosorbent assay) and UPLC-MS/MS (ultra-performance liquid chromatography-tandem mass spectrometer) analysis (Gantar *et al.* 2009; Stanić *et al.* 2011). Strains isolated from the Caribbean islands corals reefs of *Geitlerinema* (Anagnostidis & Komárek) Anagnostidis, *Leptolyngbya*, *Spirulina* Turpin ex Gomont (Gantar *et al.* 2009) and *Oscillatoria* (Stanić *et al.* 2011) were all identified as MC-LR producers. Besides MC reports associated with BBD, cyanotoxins have also been detected in planktic blooms in the Caribbean Sea. Blooms of *T. erythraeum* were observed in 1991 with reports of toxicity effects (Hawser & Codd 1992). Other cyanobacteria observed in these islands, such as *Phormidium* and *Pseudanabaena*, are potential hazards since they are also described as toxin producers (Table 2).

In the Azores, MCs have been reported in São Miguel island in three volcanic lakes associated with eutrophication scenarios (Santos *et al.* 2012; Mantzouki *et al.* 2018a). Besides MC detections, cyanotoxins producing genes (MC and CYN) have also been reported in five lakes and two hot springs (Moreira *et al.* 2011). Although cyanotoxins reports are only from São Miguel island, cyanobacteria species identified

TABLE 2. — Toxic cyanobacteria species reported in the Atlantic islands. Notes: ¹ Analytical identification on isolated cultures; ² Cyanotoxin production potential (analytical identification on environmental samples or by molecular methods). **ATX-a**, anatoxin-a; **HATX-a**, homoanatoxin-a; **APT**, aplysiatoxin; **DTA**, debromoaplysiatoxin; **LTX**, lyngbyatoxin; **MC**, microcystin; **STX**, saxitoxin; **CYN**, cylindrospermopsin; **deoxy-CYN**, deoxy-cylindrospermopsin. (For island codes correspondence see Table 1).

Reported species	Cyanotoxin(s)	References (Toxic species)	Islands
<i>Anabaena</i> Bory ex Bornet & Flahault	ATX-a ¹ , MC ¹	Park <i>et al.</i> 1993; Osswald <i>et al.</i> 2009	IS, MD, CU
<i>Anabaena cylindrica</i> Lemmermann	MC ¹	Mohamed <i>et al.</i> 2006	CU
<i>Aphanizomenon</i> Morren ex Bornet & Flahault	ATX-a ¹	Sivonen <i>et al.</i> 1989; Mohamed <i>et al.</i> 2006	CU
<i>Aphanizomenon flos-aque</i> Ralfs ex Bornet & Flahault	ATX-a ¹ , CYN ² , MC ²	Maatouk <i>et al.</i> 2002; Brient <i>et al.</i> 2008; Osswald <i>et al.</i> 2009	AZ (Corvo, Flores, São Miguel), IC, CU
<i>Aphanizomenon gracile</i> Lemmermann	CYN ¹ , STX ¹	Pereira <i>et al.</i> 2004; Kokociński <i>et al.</i> 2013	AZ (Flores, Pico, São Miguel), CU
<i>Blennothrix lyngbyacea</i> (Kützinger ex Gomont) Anagnostidis & Komárek	HATX-a ²	Méjean <i>et al.</i> 2010	BR (Bela, Cardoso, Casca)
<i>Calothrix parietina</i> Thuret ex Bornet & Flahault	MC ¹	Mohamed & Al Shehri 2007	CU
<i>Cylindrospermum</i> Kützinger ex Bornet & Flahault	ATX-a ¹	Sivonen <i>et al.</i> 1989	IS, AZ (Pico), CU
<i>Dolichospermum planctonicum</i> (Brunnthal) Wacklin, Hoffmann & Komárek	ATX-a ¹ ; CYN ²	Park <i>et al.</i> 1993; Brient <i>et al.</i> 2008	AZ (Pico, São Miguel), CU
<i>Dolichospermum sigmoideum</i> (Nygaard) Wacklin, Hoffmann & Komárek	ATX-a ¹ ; MC ¹ ; STX ¹	e.g. Sivonen <i>et al.</i> 1989; Humpage <i>et al.</i> 1994	AZ (Pico, São Miguel), CU
<i>Dolichospermum spiroides</i> (Kleban) Wacklin, Hoffmann & Komárek	ATX-a ¹ ; ATX-a(s) ¹	Park <i>et al.</i> 1993	AZ (São Miguel), CU
<i>Geitlerinema</i> (Anagnostidis & Komárek) Anagnostidis	MC ¹	Gantar <i>et al.</i> 2009	BS (San Salvador), CV, CW
<i>Hapalosiphon hibernicus</i> West & West	MC ¹	Prinsep <i>et al.</i> 1992	AZ (Corvo, Flores, São Miguel), CU
<i>Kamptonema formosum</i> (Bory ex Gomont) Strunecký, Komárek & Smarda	HATX-a ²	Skulberg <i>et al.</i> 1992	IS, AZ (São Miguel, Santa Maria, Terceira), CU
<i>Leptolyngbya</i> Anagnostidis & Komárek	MC ¹	Gantar <i>et al.</i> 2009	IS, AZ (São Miguel), CU, CV (Santiago)
<i>Limnothrix redekei</i> (Goor) Meffert	STX ¹	Pomati <i>et al.</i> 2000	AZ (São Miguel), CU
<i>Lyngbya majuscula</i> Harvey ex Gomont	APT ² , DTA ² , LTX ²	Fujiki <i>et al.</i> 1985; Aimi <i>et al.</i> 1990	IC, BS (San Salvador), CW
<i>Merismopedia</i> Meyen	MC ¹	Furtado <i>et al.</i> 2009	CU
<i>Microcoleus autumnalis</i> (Gomont) Strunecký, Komárek & Johansen	ATX-a ¹	Osswald <i>et al.</i> 2009	CU
<i>Microcystis aeruginosa</i> (Kützinger) Kützinger	ATX-a ¹ , MC ¹	e.g. Park <i>et al.</i> 1993	AZ (Corvo, Flores, São Miguel), CU
<i>Microcystis flos-aquae</i> (Wittrock) Kirchner	MC ¹	Sivonen & Jones 1999; Via-Ordorika <i>et al.</i> 2004	AZ (Flores, São Miguel), CU
<i>Nostoc</i> Vaucher ex Bornet & Flahault	MC ¹	Sivonen 1990; Oksanen <i>et al.</i> 2004	AZ (Corvo, Flores, São Miguel, Santa Maria), IC (Gran Canaria), CU
<i>Nostoc carneum</i> Agardh ex Bornet & Flahault	MC ¹	Mohamed & Al Shehri 2007	CU
<i>Oscillatoria</i> Vaucher ex Gomont	ATX-a ¹ , CYN ² , HATX-a ² , MC ²	Cadel-Six <i>et al.</i> 2007; Osswald <i>et al.</i> 2009; Mazmouz <i>et al.</i> 2010; Stanić <i>et al.</i> 2011	IS, AZ (Flores, Pico, Santa Maria, Terceira), CU
<i>Oscillatoria tenuis</i> Agardh ex Gomont	MC ¹	Mohamed <i>et al.</i> 1999; Brittain <i>et al.</i> 2000	AZ (Corvo, Faial, Flores, Graciosa, Pico, São Miguel, Terceira), CU
<i>Phormidium</i> Kützinger ex Gomont	ATX-a ¹ , HATX-a ¹ , MC ¹	Cadel-Six <i>et al.</i> 2007; Gantar <i>et al.</i> 2009	IS, BS (San Salvador), CU, CV (Santiago), CW
<i>Phormidium corium</i> Gomont ex Gomont	MC ¹	Mohamed <i>et al.</i> 2006	IC, BS (San Salvador), CW, BR (Bela, Cardoso, Casca)
<i>Planktothrix</i> Anagnostidis & Komárek	MC ²	Ernst <i>et al.</i> 2001	CV (Santiago)
<i>Planktothrix agardhii</i> (Gomont) Anagnostidis & Komárek	ATX-a ¹ ; MC ¹	e.g. Sivonen <i>et al.</i> 1989, 1990	AZ (São Miguel)
<i>Pseudanabaena</i> Lauterborn	MC ¹	Gantar <i>et al.</i> 2009	AZ (São Miguel), BS (San Salvador), CW
<i>Pseudanabaena catenata</i> Lauterborn	MC ¹	Mohamed & Al-Shehri 2015	AZ (São Miguel)
<i>Pseudanabaena limnetica</i> (Lemmermann) Komárek	ATX-a ¹	Osswald <i>et al.</i> 2009	AZ (Corvo, Flores, Pico, São Miguel)
<i>Raphidiopsis curvata</i> Fritsch & Rich	CYN ¹ ; deoxy-CYN ¹	Li <i>et al.</i> 2001	AZ (Corvo, Flores, São Miguel)
<i>Spirulina</i> Turpin ex Gomont	MC ¹	Gantar <i>et al.</i> 2009	BS (San Salvador), CW
<i>Synechococcus</i> Nägeli	MC ¹	Gantar <i>et al.</i> 2009	MD, CV (Santiago)
<i>Tolypothrix distorta</i> Kützinger ex Bornet & Flahault	MC ¹	Aboal <i>et al.</i> 2005	AZ (São Miguel)
<i>Trichodesmium erythraeum</i> Ehrenberg ex Gomont	MC ² , STX ²	Ramos <i>et al.</i> 2005; Proença <i>et al.</i> 2009	MD, IC

TABLE 2. — Continuation.

Reported species	Cyanotoxin(s)	References (Toxic species)	Islands
<i>Trichormus variabilis</i> (Kützing ex Bornet & Flahault)	MC ¹	Mohamed <i>et al.</i> 2006	AZ (São Miguel), IC
Komárek & Anagnostidis			
<i>Woronichinia naegeliana</i> (Unger) Elenkin	MC ¹	Bober & Bialczyk 2017	AZ (Corvo, Flores, Pico, São Miguel)

has ATXs, MCs, STXs and CYNs producers were observed in almost all of the Azores islands, including species such as *Aphanizomenon gracile*, *A. flos-aquae*, *Microcystis aeruginosa* (Kützing) Kützing and *O. tenuis* (Table 2).

The presence of cyanotoxin-producing cyanobacteria, even without cyanotoxins identification and report, may indicate a potential hazard. It might just take a variation in normal habitat conditions, as it was the case of the Canary Islands in 2004 (Ramos *et al.* 2005), to lead to toxic cyanobacteria blooms. With the recent climate change shifts in the regular habitat conditions, such as temperature and turbulence, are to be expected, enhancing the formation of cHABs as well as toxin production and release (Townhill *et al.* 2018).

GLOBAL WARMING AND CLIMATE CHANGE IMPACTS IN CYANOBACTERIAL COMMUNITIES

Climate change has affected phytoplankton communities and dynamics worldwide, as seen in many reports recently published in the scientific literature (e.g. Mantzouki *et al.* 2018b; Townhill *et al.* 2018). Most of these studies point out the importance of temperature and nutrients as the main drivers of cyanobacteria dominance on phytoplankton communities and the occurrence of cHABs. With global warming and temperature rising some cyanobacteria species may have an advantage since they can grow and develop better at higher temperatures than most microalgae (e.g. $\geq 25^{\circ}\text{C}$), that generally prefer lower temperatures (Paerl & Huisman 2008, 2009; Paerl 2018). In colder regions, global warming is affecting aquatic ecosystems by freezing and unfreezing at different periods (usually shorter freezing periods) or by unfreezing lakes permanently (Paerl 2018). Changes in water vertical mixing can favor cyanobacteria species with aerotopes and/or heterocytes over other phytoplankton organisms under more strongly stratified waters due to their ability to vertical migration and resistance to nitrogen-limited conditions (Lürling *et al.* 2013; Paerl 2018). The increase of cyanobacterial blooms in future years, associated to global warming, are indeed more likely to be due to cyanobacteria's ability to migrate vertically, rather than its higher growth rate at higher temperature (Lürling *et al.* 2013).

Besides global warming, climate changes also bring altered precipitations, droughts and catastrophic events that likewise affect phytoplankton growth; however, cyanobacteria have again an advantage leading to their overdevelopment regarding microalgae. With changed precipitation regimes, strong winds and droughts, nutrients become more available for cyanobacteria essentially due to water masses stratification

(O'Neil *et al.* 2012). Cyanobacteria respond to various factors and bloom formations are affected by water vertical stratification, temperature, and increased nutrient supply as mentioned before, and also by winds, upwelling, and currents in the ocean (Townhill *et al.* 2018). These last ones are all associated with vertical mixing and higher nutrient availability, which as explained before, leads to cyanobacteria development and blooms formations (Townhill *et al.* 2018; Paerl 2018).

Atlantic Ocean islands are expected to be affected by these changes, however, is not that easy to define exactly what will happen regarding cHABs on each island. Generally, it is expected that will worsen due to the changes in environmental drivers as mentioned earlier that ultimately will affect cyanobacteria species distribution, abundance, and toxin production.

Species distribution may be impacted by these climate changes, implying that cyanobacteria restricted to warmer temperature zones may expand to colder regions. Species present only in regions with temperatures higher than 20°C may expand to regions that presently have more moderate temperatures (Fig. 4A). In fact, in recent decades temperatures rises matches with increased phytoplankton in the North of the Atlantic Ocean (Bresnan *et al.* 2013).

Cyanobacteria dynamics will change, not only concerning other phytoplankton groups but also within cyanobacteria groups, favoring species that adapt better at higher temperatures and resist better to oscillations (precipitation, winds, temperature, and nutrients). One of the biggest concerns with climate change and anthropogenic influences is the emerging of cyanotoxin producing species and the increase of bloom events by these species, called cHABs. With the temperature rising it is expected that blooms of highly toxic strains will be more frequent, with loss of toxin diversity production (Mantzouki *et al.* 2018b). In the last years CYN studies regarding species, toxicity, occurrence, and toxic events (Rzyski & Poniedzialek 2014) have been more common, unlike the well-known and common MC, evidencing climate change consequences on toxicity diversity loss (Mantzouki *et al.* 2018b). By the exposure to higher concentrations and/or more toxic cyanotoxins, future cHABs will bring bigger risks to aquatic life and humans, leading to biodiversity loss, health, and economic costs (Mantzouki *et al.* 2018b; Burford *et al.* 2020). Another point of concern should be the lack of information regarding benthic cyanobacteria and the possibility of blooms development and toxin production, for which very little is known neither how climate change could affect them (Burford *et al.* 2020).

Islands should be a key priority regarding global warming and cHABs, since climate change could be harsher in islands, due to their geographical isolation and smaller geographical

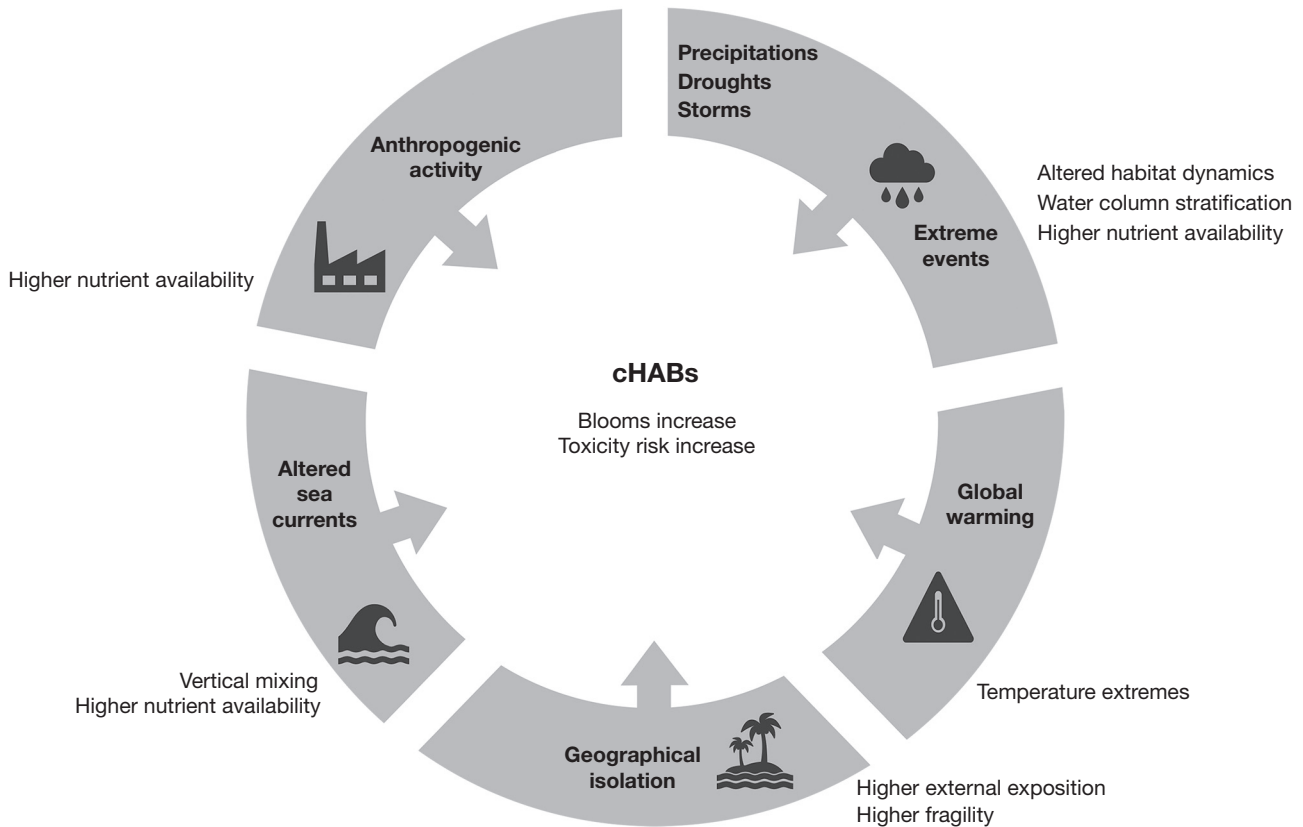


FIG. 5. — Environmental conditions contributing to the occurrence of cHABs in insular ecosystems.

sizes that makes them more exposed to external influences and extreme events (Nurse *et al.* 2014). So, it is expected that the consequences of global warming, previously stated, will be enhanced in islands (Fig. 5).

MONITORING AND PREVENTION

Considering the expected increase in cHABs in the future it is crucial to think about monitoring and preventing actions to avoid intoxication events with impacts at environmental, health, and economic levels (Townhill *et al.* 2018). Therefore, prevention actions should be implemented to avoid cyanobacteria blooms. Several measures have been applied, from nutrients influx control to biological, chemical, and hydrodynamics control (Huisman *et al.* 2018). Some of these strategies are more effective than others, however, none of them are completely effective and each water mass and cyanobacteria bloom is different and caused by different drivers, that should be considered when planning a multidisciplinary mitigation and prevention action.

CONCLUDING REMARKS

This review compiles available information on cyanobacteria and cyanotoxins presence in Atlantic Ocean Islands, gathering over 400 taxa from 35 islands. Available data came from various

sources, including earlier scientific expeditions notes to more detailed and specialized works, such as scientific articles, conference proceedings, and technical reports. In addition to the variety of information sources, the different sampling efforts and methodologies used for sampling and identification, either by classic taxonomical classification (inconsistent throughout the years) or molecular techniques (16S, metabarcoding, etc.), partially overcome by cyanobacteria nomenclature update according to the most recent literature, limited the analysis and conclusions of this review. Nevertheless, this review clearly shows that Atlantic Ocean islands harbor a great diversity of cyanobacteria, but their study in insular environments is still very limited in several islands and habitats. Besides understudied islands, some environments are also understudied, such as brackish, thermal, and terrestrial. For this reason, understudied islands and environments should be a focus of identification, isolation, and bioprospecting studies. Sampling, isolating, and characterization of cyanobacteria, consequently, the creation of culture collections will support complex studies in specific strains to increase the knowledge on cyanobacteria diversity, distribution, morphology, physiology, and biochemistry.

Although the recognition of distribution patterns of cyanobacteria was influenced by the referred methodological limitations and the lack of studies in some regions (e.g. South Atlantic islands, Cape Verde and several Caribbean islands), our results point to a higher cyanobacteria species richness at mid-latitude regions and a significant proportion of unique taxa in different climatic zones.

Our review also highlights the fragility of islands facing external pressures, such as human disturbances and global warming. Taking this into consideration we heighten the importance of mitigation methods and actions due to climate change effects on cyanobacteria communities. Further studies should be considered to better understand these risks, to avoid cHABs, and to create guidelines for monitoring and risk management in these insular, liable, environments.

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APPENDIX

APPENDIX 1. — Cyanobacteria biodiversity and distribution in different habitats of the Atlantic Ocean's islands (NGS: next generation sequencing). This document is available at the following address: <http://sciencepress.mnhn.fr/sites/default/files/documents/en/appendix1.xlsx>