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REVIEW PAPER

Everything is not everywhere: a tale on the biogeography of cyanobacteria

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Abstract Microrganisms such as cyanobacteria have been often considered as exhibiting wide distribution mainly driven by environmental heterogeneity. Recently, however, new findings have evoked the role of previously neglected processes, such as dispersal limitation, determining the distribution of a wide range of microorganisms, including cyanobacteria. Here, we reviewed the biogeographic patterns of cyanobacteria with focus on molecular data and the evidences from the published literature for the processes driving these patterns. Also, considerations are made about concept of species, discordances in the taxonomic concepts, and level of taxonomic resolution, and how these affect the biogeographic study of cyanobacteria. From a overview, it can be observed that both environmental and historical factors are important to structure cyanobacteria diversity across time and space. Moreover, different species may exhibit significant differences in their distribution patterns, from possibly cosmopolitan species to other endemic species. However, distribution patterns are closely dependent on the concept of species, besides the taxonomic resolution, spatial and environmental scales, and the biases of the molecular methodologies applied in the studies. Thus, efforts to broaden sampling and sequencing of unknown and less-known species, as well as geographic regions and habitats poorly exploited, are crucial for a better understanding of cyanobacteria biogeography.

Keywords Microbial cosmopolitanism · Microbial diversity predictors · Phylogeography · Microbial ecology · Cyanoprokaryota

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Introduction

Cyanobacteria are a diverse group of microrganisms characterized as being oxygenic photosynthetic bacteria that possess chlorophyll *a* (Castenholz, 2001). Cyanobacteria possess a high ecological plasticity, thanks to which they occur in varied, often even extreme, habitats (Whitton & Potts, 2000). This group was responsible for critical events throughout the evolutionary history of life on Earth, such as the history of Earth-surface oxygenation (Lyons et al., 2014; Rasmussen et al., 2008; Sessions et al., 2009) and the evolution of eukaryotic cell through

endosymbiosis (Margulis, 1970; Woese, 1987; McFadden, 2014). In addition, cyanobacteria play key roles in the ecosystems and biogeochemical cycles (Capone et al., 1997; Liu et al., 1997). Furthermore, in aquatic ecosystems, some taxa are capable of forming blooms, events characterized by the sudden increase in the abundance of one or some taxa in the environment. Also, many species from this group are able to release toxins (Carmichael, 2001; Paerl & Huisman, 2009), which can affect aquatic fauna as well as human populations. However, in spite of these negative impacts on ecosystems, cyanobacteria are economically important due to their potential use in pharmaceutical, food, and biotechnological industries (e.g., Singh et al., 2005; Gantar & Svircev, 2008; Gerwick et al., 2008; Pfeiffer et al., 2011; Zanchett & Oliveira-Filho, 2013).

Most research on cyanobacteria is guided by evolutionary, ecological, ecotoxicological, biochemical, and taxonomic concerns (for a review on common investigation on cyanobacteria see Sciuto & Moro, 2015). With the current development and improvement of molecular techniques and tools in microbial ecology, the microbial biogeography field has been deeply investigated (see Bell et al., 2005; Martiny et al., 2006, Ramette & Tiedje, 2007; Woodcock et al., 2007; Bell, 2010; Hanson et al., 2012; Naselli-Flores & Padisák, 2016; Padisák et al., 2016), including biogeography studies with focus on cyanobacteria (see Moreira et al., 2013). The methods for biogeographic studies in cyanobacteria and cyanotoxins are based on the identification and subsequent phylogenetic analyses of the isolates or environmental samples using predetermined genetic markers to establish their genetic diversity and geographic interaction (Neilan et al., 2003; Moreira et al., 2012). Thus, these studies are generally based on the discovery of new genera or species in new environments (e.g., Komárek, 1985; Couté et al., 2004; Couté & Bouvy 2004); endemisms (e.g., Sompong et al., 2005; Taton et al., 2006; Jungblut et al., 2010); potentials of dispersion and invasion (e.g., Padisák, 1997; Dyble et al., 2002; Wiedner et al., 2007; Vidal & Kruk, 2008; Sukenik et al., 2012; Wilk-Woźniak et al., 2016); and spatial distributions of species, populations and communities related to spatial and environmental variables (e.g., Papke et al., 2003; Drakare & Liess, 2010; Chamberlain et al., 2014).

The main goal of biogeography is to describe how species are distributed and the driving forces of these distribution patterns, and *prokaryotic biogeography* has been previously defined as the scientific field that documents the spatial distribution of prokaryotic taxa (Archaea and Eubacteria) in the environment at local, regional and continental scales (Ramette & Tiedje, 2007). To detect biogeographic patterns for microorganisms is crucial for understanding the distribution of biodiversity, since microorganisms are the most abundant and diverse group of Earth, being the life-support system of the planet (Pace, 1997; Hug et al., 2016; Locey & Lennon, 2016). Despite the classical idea of pure environmental selection on microbial distributions pervading the ecological literature for a long time (Baas-Becking, 1934), recent studies have evoked the existence of geographic isolation and dispersal barriers for some microbial groups from a variety of habitats, such as heterotrophic bacteria from soils (Cho & Tiedje, 2000), thermophilic cyanobacteria (Papke et al., 2003) and archaea (Whitaker et al., 2003) from hot springs. These recent hypothesis arguing against "cosmopolitan microbial rule" indicate a still very limited understanding of the mechanisms involved in microbial biogeography and how patterns of distribution vary among taxonomic groups and habitats, the main issues currently discussed in microbial ecology.

Despite the increased interest in exploring distribution patterns of cyanobacteria, however, a key issue in biogeography challenges the research in this field: the species concept. Since biogeography is concerned with the distribution of *species*, a well-defined species concept is required. Besides the existence of more than one concept of species (Dobzhansky, 1937; Wright, 1951; Slatkin, 1987), the concept of bacterial species in particular is considerably obscure, since its definition is typically defined coarsely (e.g., as > 97% similarity of 16S or 18S ribosomal RNA genes) (about bacterial species concept see Konstantinidis & Tiedje, 2005; Achtman & Wagner, 2008; Fraser et al., 2009; Caro-Quintero & Konstantinidis, 2011). Apart from these issues, cyanobacteria have a particular characteristic: the fact that they have traditionally been studied in botany and taxonomically classified in the same way as algae and plants. These issues, in addition to the scarcity of qualified professionals to identify and classify taxa, may potentially hamper studies of the group (Rejmánková et al., 2004), including

biogeographic studies (as we will discuss throughout this review). This review explores the current status of the field of biogeography of cyanobacteria and highlights joint distribution/population genomics/biodiversity/workflows that aim to overcome some of the challenges commonly found in this field.

Cyanobacterial species concept

Although cyanobacteria have been widely studied in scientific literature, mainly with respect to aspects such as public health and bloom formation (Graham et al., 2009), little attention has been paid to their biodiversity (Nabout et al., 2013). These shortcomings in estimation of diversity and taxonomic classification are worsened by the confusion and overlap of the two taxonomic systems used to classify cyanobacteria: the Botanical Code and the Prokaryotic Code. As mentioned above, cyanobacteria were initially studied in botany, and for legacy reasons the International Code of Nomenclature for algae, fungi, and plants (Botanical Code) (McNeill et al., 2012) is still used for describing cyanobacteria in addition to the International Code of Nomenclature of Prokaryotes (Prokaryotic Code) (Parker et al., 2015). The history of cyanobacterial research in these two fields has also caused some discordance in taxonomic concepts and resulted in long discussions concerning the application of nomenclatural rules for cyanobacteria (Gaget et al., 2011; Oren, 2011; Oren & Garrity, 2014). Currently, the number of described cyanobacteria in the literature is controversial and the estimates range from 2000 (Sant'Anna et al., 2006) to 8000 species (Guiry, 2012) distributed among more than 300 genus. Nabout et al. (2013), in order to assume the underestimation of species, have estimated the number of unknown cyanobacteria species by using three models of discovery curves, and showed that the best model estimated a total of 6280 species (the number of species already described is 43% of this total).

With the huge advances that recent technologies have brought to microbiology, especially in the field of genomics, recent studies have focused their efforts on revising the taxonomy of cyanobacteria with a view to correcting mistakes caused by traditional taxonomics and clearing out the complicated evolutionary relationships of polyphyletic groups (e.g., Komárek, 2006; Komárek & Mareš, 2012; Komárek et al., 2014;

Komárek, 2016). Today, the combination of microscopic data with molecular information is the most appropriate method for systematic and ecologic studies (Komárek et al., 2014; Komárek, 2016). More specifically, is considered as species within a single genus, those cyanobacterial strains or populations that belong to the "same genotype and morphotype with stable phenotypic features, and more or less stable and distinct ecological limits" (Komarek & Mareš, 2012; Komárek, 2016). Since the earliest-described species lack genetic information, previously described species are also undergoing thorough taxonomic revision (Castenholz, 2001; Komárek, 2006, 2016). Taxonomic revisions at the suprageneric level are also underway (e.g., Mareš, 2017), and currently it seems that the best defined way how to separate cyanobacterial species using molecular markers is the use of the 16S–23S internal transcribed spacer (ITS) region (Erwin & Thacker, 2008; Perkerson et al., 2011; Osorio-Santos et al., 2014).

It is also important to mention that, even if new efforts are made to access the genetic diversity of cyanobacteria, relating genetic diversity to a species concept is not easy. Cyanobacteria, in the same way as other prokaryotic organisms, have a set of essential genes (core genome) highly conserved and resistant to horizontal transfer (Shi & Falkowski, 2008; Larsson et al., 2011) and at same time a set of nonessential genes (accessory genome), that are more frequently subject to horizontal gene transfer and plays an important role in generating molecular diversity in cyanobacteria (Zhaxybayeva et al., 2006). Moreover, genome plasticity in cyanobacteria is evidenced by the broad distribution and hypervariability of mobile genetic elements (mainly insertion sequences), which can amount up to 10.95% of some genomes (Lin et al., 2010). Therefore, if populations of a same cyanobacterial species must have the same genotype, it is not trivial to think of which gene (or genes), and which cutoff value of nucleotide similarity, are more appropriate to consider. Phylogenetic reconstructions based on a single gene may be problematic, for instance, since they result in gene trees rather than species trees, ignoring the possibility of horizontal transfer which has been documented in prokaryotic rRNA operons (Ueda et al., 1999; Yap et al., 1999; Mareš, 2017).

Despite the genomics to be currently the most promising framework for revising the taxonomic classification of cyanobacteria, it is worth mentioning

that these field has been moving forward at a pace that is relatively slower than currently observed for some of the other bacterial phyla (Alvarenga et al., 2017). Nowadays, the number of cyanobacterial genomes amounts for approximately 0.6% of all prokaryotic genomes available (Alvarenga et al., 2017). About 400 cyanobacterial genomes are available in public databases, in contrast to more than 30,000 complete genomes available for strains classified in 50 bacterial and 11 archaeal phyla (Land et al., 2015). Cyanobacteria, therefore, are still severely underrepresented in genomic databases when compared to other prokaryotes, and the currently available cyanobacterial genome databases are still lacking in taxonomic, environmental, and geographic diversity (Alvarenga et al., 2017). This scenario, in addition to providing an incomplete picture of this phylum, prevents the expansion of knowledge of the molecular biology of cyanobacteria, since sequences from neglected taxa may bring to light answers to meaningful questions (Richards, 2015).

From obtaining new genetic data of cyanobacteria in order to get closer to their real biodiversity, not only can their phylogeny be better resolved, but new approaches in ecological studies may be explored, such as in phylogenetic community ecology, phylogeography, and of course biogeography. As mentioned briefly above, biogeography is very sensitive to the species concept and taxonomic resolution, both closely related to access to biodiversity. This is because key concepts studied in biogeography are defined from a species definition: habitats/niches are defined as a particular combination of resources and conditions necessary for a particular species (Tiedje, 1993), and both dispersion and ecological drift (including here speciation and extinction) depends on the size of the populations (Slatkin, 1987), which in turn will depend on the definition of specie adopted. Considering the processes involved in the biodiversity distribution mentioned above, in the following sections, we present a synthesis of the biogeography studies on cyanobacteria, and the evidences presented in the literature of the driving factors shaping cyanobacteria distribution. At the same time, we made considerations regarding species concept, taxonomic resolution and other issues involved in the development of this research field. Finally, we discuss perspectives for this field and suggestions for future

investigations that will contribute to a better understanding of the biogeography of cyanobacteria.

Environmental selection (current biotic and abiotic conditions)

One of the processes involved in the distribution of biodiversity widely studied in biogeography is the environmental selection (or environmental filtering), in which abiotic and biotic (biological interactions) conditions selects against species with different tolerances and habitat preferences. This process traditionally was thought to be a major mechanism structuring communities (Stein et al., 2014), and widely explored in ecological studies, mainly on animals and plants. In microbial ecology, the role of environmental heterogeneity also was thought to be the main factor shaping bacterial distribution, assumption known as Baas-Becking hypothesis (Baas-Becking, 1934). In this fundamental paradigm, *everything is everywhere, but environment selects* (Baas-Becking, 1934), the first proposition implies that microorganisms have dispersal abilities so high that the effects of past processes are suppressed; and the second one assumes that the current environmental characteristics determine the microbial distribution in the ecosystems. Although the idea of distribution purely selected by environmental conditions is currently under intense debate and review (as we will show in more detail in the following sections), a lot of evidence in the literature shows an important role of environmental heterogeneity in the biogeographic distribution of cyanobacteria.

At the same time, as cyanobacteria present a broad range of metabolic capacities that enable them to deal with a range of environmental conditions (Vasas et al., 2010)—this group exhibits high niche specialization (Whitton & Potts, 2000)—then, the occurrence of distributions restricted to certain habitat types can highlight the role of environmental selection. Several studies have shown that, in fact, the environmental heterogeneity influences the distribution of cyanobacteria in a variety of spatial scales and ecosystems (Tables 1 and 2). At local and regional spatial scales, patterns of cyanobacteria distribution in aquatic ecosystems are commonly related to the concentration of nutrients and variables related to solar radiation, such as water transparency and water body depth (e.g., Drakare & Liess, 2010; Tian et al., 2012; Chamberlain

Table 1 Examples of 16S–23S rRNA gene target and microscopy-based studies that have found nonrandom distributions of cyanobacterial communities

Approximate scale (km)	Habitat	Identification method	Correlated with	Endemism	Reference
3500	Antarctic free-ice terrestrial sites	Molecular	Vegetation cover	✔	Namsaraev et al. (2010)
900	Swedish lakes	Molecular	Environmental variables (total organic carbon, biomass of eukaryotic phytoplankton, pH and conductivity)		Drakare & Liess (2010)
260	Hot springs, Thailand	Microscopy	Temperature and barriers to the dispersal of some taxa	✔	Sompong et al. (2005)
140	Microbial mats in lakes of Eastern Antarctica	Microscopy and molecular	Environmental variables (salinity, light intensity and depth)	✔	Taton et al. (2006)
80	Nansi Lake, China	Microscopy	Environmental variables (temperature and phosphorus)		Tian et al. (2012)
55	Aquatic habitats, High Arctic Canada	Molecular	Global distribution of low-temperature cyanobacterial ecotypes throughout the cold terrestrial biosphere		Jungblut et al. (2010)
40	Hongze Lake, China	Microscopy	Environmental variables (water temperature, dissolved oxygen, nitrate, chemical oxygen demand, transparency and total nitrogen)		Ren et al. (2014)
40	Coastal waters and sediments of the Big Island, Hawaii	Molecular	Habitat type (sediments and water) and environmental variables (temperature, salinity, dissolved oxygen, chlorophyll a, pH, total suspended matter, nitrogen stable isotope, organic matter and mean sediment size)		Chamberlain et al. (2014)
35	Batticaloa Lagoon, Sri Lanka	Microscopy	Environmental variables (nitrate, total phosphorus and turbidity levels)		Harris et al. (2016)
20	Habitats across Taylor Valley, Antarctica	Molecular	Eolic processes	✔	Michaud et al. (2012)
10	Dongping Lake, China	Microscopy	Environmental variables (temperature, chemical oxygen demand and concentration of inorganic nitrogen)		Lu et al. (2013)

et al., 2014; Ren et al., 2014; Harris et al., 2016). Similarly, in terrestrial environments, the physical–chemical characteristics of soils and sediments appear to be important factors shaping the distribution of cyanobacteria (e.g., Garcia-Pichel et al., 2001; Thomasa & Dougil, 2006; Chamberlain et al., 2014).

Cyanobacterial blooms in aquatic ecosystems also show how changes in local and regional environmental characteristics can affect and alter the distribution patterns of these organisms. Events of cyanobacteria blooms show to what extent environmental variables (specifically the excess in nutrient concentrations and

temperature increase) (Paerl et al., 2001; Paerl & Paul, 2012; Paerl & Otten, 2013) can rapidly affect and change the structure of cyanobacterial communities. Some genera in particular are widely studied because of their ability to form blooms (toxic or not) in freshwater environments, such as *Microcystis*, *Anabaena*, *Cylindrospermopsis*, and in marine ecosystems, such as *Lyngbya*, *Synechococcus*, *Trichodesmium* (Rastogi et al., 2015). On tropical blooms, for example, a meta-analysis showed that *Microcystis* blooms were more associated with higher total nitrogen concentrations, while

Table 2 Examples of molecular-based studies that have found nonrandom distributions of cyanobacterial populations or ecotypes

Habitat	Taxon	Taxon characterization	Identification method	Correlated with	Reference
Hot and cold deserts	*Chroococcidiopsis*	Extremophile cyanobacteria	multilocus sequences	Ancient evolutionary legacy	Bahl et al. (2011)
Strains of four continents from different habitats	*Cylindrospermopsis raciborskii*	Filamentous cyanobacteria; heterocyst and akinetes-forming; potentially forming harmful blooms	16S-23S ITS-1	Recent spread across the American and European continents from restricted warm refuge areas/recent colonization of Australia by African strains	Gugger et al. (2005)
Isolates from Africa and Europe			ITS1, PC-IGS, nifH and rpoC1	Geographic cluster distribution	Haande et al. (2007)
Aquatic samples from all continents			16S rRNA, 16S-23S ITS-L, 16S-23S ITS-S and rpoC1	Clustering of the strains due to geographic origin/recent invasion in the European temperate environments	Moreira et al. (2011)
Freshwater systems from different continents			16S rRNA and HIP1 PCR profiles	Geographic cluster distribution	Neilan et al. (2003)
Thermal areas	*Mastigocladus laminosus*	Thermophilic filamentous cyanobacteria; heterocyst and akinetes-forming	multilocus sequences	Dispersal barriers and geographic isolation by distance	Miller et al. (2007)
Marine benthic microbial mats	*Microcoleus chthonoplastes*	Filamentous cyanobacteria	16S rRNA	No dispersal barriers/cosmopolitan distribution	Garcia-Pichel et al. (1996)
Different habitats from three continents	*Microcoleus vaginatus*	Filamentous cyanobacteria	16S rRNA and 16S–23S ITS	Dispersal barriers and allopatric speciation	Dvořák et al. (2012)
East-African water bodies	*Microcystis aeruginosa*	Colonial cyanobacteria; potentially forming harmful blooms	PC-IGS and ITS1 rDNA	Clustering of the strains due to geographic origin	Haande et al. (2007)
Strains from five continents			mcy gene cluster (mcyA, mcyD and mcyG)	Geographic cluster distribution/evidence of positive selection in mcy genes	Moreira et al. (2013)
Water bodies from Israel			mcyD and mcyA genes	Environmental, geospatial and land use factors	Marmen et al. (2016)
Samples from all continents			rDNA ITS	Intercontinental dispersal/cosmopolitan distribution	van Gremberghe et al. (2011)
Arctic ecosystems from Europe and Canada	*Phormidium autumnale*	Filamentous cyanobacteria	16S rDNA and 16S–23S rDNA ITS	Rate of colonization relatively high/cluster of genotypes in the phylogenetic tree according to their occurrence in similar habitats	Sukenik et al. (2012)

Table 2 continued

Habitat	Taxon	Taxon characterization	Identification method	Correlated with	Reference
European freshwater habitats	*Planktothrix*	Filamentous cyanobacteria; gas vacuoles present	mcy gene cluster	Spatial isolation favoring the genetic divergence	Kurmayer and Gumpenberger (2006)
Atlantic and Pacific oceans	*Prochlorococcus*	Unicellular picocyanobacteria	16S-23S rRNA ITS	Environmental selection and dispersal limitation	Martiny et al. (2009)
Seawaters around the world	*Synechococcus*	Unicellular picocyanobacteria	Multilocus sequences	Environmental selection	Mazard et al. (2012)
Gulf of Aqaba, Red Sea			rpoC1 gene	Cyanophage infection	Mühling et al. (2005)
Hot springs			16S rRNA and 16S-23S ITS	Genetic drift by geographic isolation	Papke et al. (2003)
Temperate-zone lakes and the brackish Baltic Sea	*Synechococcus and Prochlorococcus*	Unicellular picocyanobacteria	16S rRNA and ITS-1	Ecosystem-dependent adaptive radiation	Ernst et al. (2003)
Diverse marine ecosystems			16S-23S rRNA ITS	Environmental selection	Huang et al. (2012)

Cylindrospermopsis blooms were more associated with higher maximum temperatures (Mowe et al., 2015). Also, environmental changes on a global scale (e.g., global warming) may potentially alter patterns of cyanobacterial blooms. More details on this issue could be found in the section: "Invasions and Global Climate Change".

In extreme environments, cyanobacteria exhibit remarkable adaptability, notwithstanding the adverse environmental conditions of most inhospitable ecosystems in the Earth, including the frozen regions of the poles (e.g., Taton et al., 2006; Wood et al., 2008; Namsaraev et al., 2010), hypersaline environments (see Oren, 2015), and, on the other extreme, the high temperatures of hot springs (e.g., Papke et al., 2003; Miller et al., 2007; Ionescu et al., 2010). These commonly isolated ecosystems provide appropriate scenarios for assessing biogeographic patterns of distribution of highly specialized groups. In the polar environments, the distribution of cyanobacteria has been correlated with aeolian processes (Michaud et al., 2012), salinity (Jungblut et al., 2005) and soil chemical characteristics (Wood et al., 2008), whereas in thermal springs areas cyanobacteria distribution shows a relation with water temperature (Sompong et al., 2005).

Biotic variables (such as the abundance and richness of other organisms) may indicate that biological interactions are acting as important factors shaping cyanobacteria distribution. This relationship has already been studied and evidenced both in studies with experimental approach as well as through field data (e.g., Sullivan et al., 2003; Mühling et al., 2005; Agawin et al., 2007; Van Wichelen et al., 2010; Apple et al., 2011; Sønstebø & Rohrlack, 2011). A study specifically evaluating the diversity of *Synechococcus* in marine ecosystems (Mühling et al. 2005), for example, found evidence that viral infection may play an important role in determining the success of different *Synechococcus* strains. Positive and negative

interactions with herbivores also influence cyanobacterial distribution patterns. For instance, copepods may facilitate cyanobacteria (Hong et al., 2013) and high abundances of generalist herbivores (e.g., *Daphnia*) can control cyanobacterial blooms when released from planktivorous fish predation (Sarnelle, 2007). Also, cyanobacterial blooms occurring in response to eutrophic conditions in water bodies may also be followed by associations with heterotrophic bacteria, several being capable of enhancing cyanobacterial growth (Berg et al., 2009).

In extreme environments such as poles and hot springs, biological interactions also play an important role in cyanobacteria distribution patterns. In the Antarctic continent, a study has observed an increase in the diversity of cyanobacteria from sub-Antarctic to continental Antarctica (Namsaraev et al., 2010), a pattern that could be explained by the disappearance of the vegetation cover since plants and mosses limit the amount of resources (nutrients available and light) for cyanobacteria. At the other extreme, in the alkaline hot springs of Yellowstone National Park, a strong negative association between the relative abundances of cyanobacteria and *Chloroflexi* (non-sulfur green bacteria) shows a likely competitive interaction between these two groups, possibly by habitat and/or limiting resources (Miller et al., 2009).

Thinking about continental and global distribution of cyanobacterial species, some taxa are studied because of their worldwide distributions. Before highlighting some of these studies, however, some terms used need to be clear. In biogeography, species considered as *cosmopolitan* are characterized by global distribution or distribution spanning several biogeographic provinces (Dijoux et al., 2014). It is important to mention here that this definition, which will be used henceforth, does not automatically imply in species that have highly efficient means of dispersal by being carried by wind or water (Fenchel & Finlay, 2004), but only concerns the distribution pattern seen today (dispersal abilities will be covered in the next section). Also, we will use the *subcosmopolitan* term, which was suggested by Padisák (2003) in order to distinguish these species from those cosmopolitan species, global occurrence of which is related to certain environments corresponding to species-specific adaptations.

Temperature is one of the majors studied factors shaping cyanobacteria distribution at global scales,

and some subcosmopolitan species are restricted to the warmest or coldest climatic regions. Pantropical species are those that occur only roughly between the two Tropics and some cyanobacteria species found in this group are all *Cylindrospermopsis* species (except *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya & Subba Raju; more about this species in the subsequent sections), *Arthrospira fusiformis* (Voronikhin) Komárek & J.W.G. Lund, *Anabaena fuellebornii* Schmidle, *Anabaena iyengarii* Bharadwaja, *Anabaena leonardii* Compère, *Anabaena oblonga* De Wildeman and *Anabaenopsis tanganyikae* (G.S. West) Woloszynska & V.V. Miller (Padisák, 2003). Well-known temperate species, on the other hand, appear to be restricted to temperate zones (Hoffmann, 1996; Vyverman, 1996), like *Planktothrix rubescens* (De Candolle ex Gomont) Anagnostidis & Komárek, *Limnothrix redekei* (Goor) Meffert, *Dolichospermum solitarium* (Klebahn) Wacklin, Hoffmann et Komárek, *Dolichospermum flos-aquae* Lyngbye Brébisson ex Bornet et Flahault) Wacklin, Hoffmann et Komárek, *Dolichospermum lemmermannii* (Richter in Lemmermann) Wacklin, Hoffmann et Komárek, *Anabaenopsis arnoldii* Aptekar, *Anabaenopsis milleri* Voronichin, *Aphanizomenon flos-aquae* Ralfs ex Bornet & Flahault and *Cuspidothrix issatschenkoi* (Usachev) P.Rajaniemi, Komárek, R.Willame, P. Hrouzek, K.Kastovská, L.Hoffmann & K.Sivonen.

Global distributions of cyanobacteria in the extreme cold environments, or cryoenvironments, have also received attention recently (e.g., Taton et al., 2006; Wood et al., 2008; Namsaraev et al., 2010). Based on clone-library and phylogenetic analysis (16S rRNA), Jungblut et al. (2010) evaluated the global distribution of cyanobacteria by comparing communities from the North America (High Arctic Canada) with those from analogous sites in Antarctica. This study have showed that several of the High Arctic ribotypes were found to be > 99% similar to Antarctic and alpine sequences. Moreover, more than 68% of all identified ribotypes at each site matched only cyanobacterial sequences from perennially cold terrestrial ecosystems, and were < 97.5% similar to sequences from warmer environments. These results show a subcosmopolitan distribution of ecotypes from different cyanobacterial taxa that, although they have a global distribution, they are highly specialized and adapted to the extreme cold conditions of the poles.

Some species of cyanobacteria that present subcosmopolitan distribution are of particular interest since specific strains are capable of forming harmful blooms. Among these, *Microcystis aeruginosa* (Kützing) Kützing is a bloom-forming freshwater-type cyanobacteria that abounds in eutrophic and hypertrophic freshwater bodies worldwide (Chorus & Bartam, 1999; de Figueiredo et al., 2006; Kardinaal et al., 2007; Vareli et al., 2009). This species has already been studied in biogeography and phylogeography and a huge of evidences of a subcosmopolitan distribution is found in the literature (Haande et al., 2007; Van Gremberghe et al., 2011). Studies analyzing populations from distinct geographic locations have revealed a high degree of intraspecific genetic similarity, indicating a robust species definition for this cyanobacterium, and this outlook was corroborated in studies using distinct molecular markers and taxonomic resolutions, such as the 16SrRNA marker (Neilan et al., 1997), cpcBA-IGS marker (Bittencourt-Oliveira et al., 2001), 16S-23S ITS marker (Haande et al., 2007; Van Gremberghe et al., 2011) and PC-IGS marker (Haande et al., 2007).

Van Gremberghe et al. (2011) studying several *Microcystis* ITS sequences from worldwide suggest a truly cosmopolitan distribution for this cyanobacterium, and interestingly, no genetic structuring according to climate conditions was found (several *Microcystis* ITS types were detected in a wide range of climates, indicating a broad tolerance or capacity for rapid local adaptation). Van Gremberghe et al. (2011) argue that is more plausible that the genetic structure of *Microcystis* populations is driven by a recent global expansion and founder effects that arise whenever new habitat patches are created (Boileau et al., 1992), which are then colonized by a random selection of strains from regional or possibly global sources. The rapid local adaptation in a wide array of environmental conditions may be a result of the genome plasticity of *M. aeruginosa* (Frangeul et al., 2008), allowing new genetic interactions and higher variance on which natural selection can act. Also, de novo mutations might be involved in rapid adaptation to novel environments given the large population sizes and short generation time of *M. aeruginosa* (van Gremberghe et al., 2011). Indeed, the distribution of nonneutral genes of *M. aeruginosa* has already been related to habitat specificity, for example to land use (Marmen et al., 2006, using the *mcyD* and *mcyA*

genes), and an evidence of local expansion of *M. aeruginosa* as response to environmental adaptation was recently found (using a multilocus approach) (Tanabe & Watanabe, 2011).

Two groups of well-studied picocyanobacteria, *Synechococcus* and *Prochlorococcus*, also provide some evidences about processes that might structure populations on a global scale. *Synechococcus* and *Prochlorococcus* are marine cosmopolitan genera of cyanobacteria and the major primary producers in the world's oceans (Li, 1994). The two genera are distinguishable by their possession of dissimilar light-harvesting apparatus (Ting et al., 2002) and even based on 16S rRNA gene (a very conservative genome region), several lineages within *Synechococcus* have been described (Fuller et al., 2003), while other potential lineages have been designated based on others genomic regions, such as ITS and *ntcA* sequences (Ahlgren & Rocap, 2006; Penno et al., 2006). It is widely known that different environmental pressures act not only between these two taxa, but also within each taxa, structuring well-known ecotypes (populations genetically different) in space according to different habitat preferences (e.g., Ernst et al., 2003; Zwirglmaier et al., 2008; Martiny et al., 2009; Ahlgren & Rocap, 2012; Huang et al., 2012; Mazard et al., 2012; Shibl et al., 2014) (Table 2). In a study on a global scale (Zwirglmaier et al., 2008), for instance, the distribution lineages (based on 16S rRNA) of these two cyanobacterial groups were related to environmental variables and, interestingly, *Prochlorococcus* appeared to be more influenced by the physical parameters (temperature and depth), while *Synechococcus* by chemical parameters (nutrients). Genetically distinct clades based on ITS sequences with very broad distributions have also been detected (Rocap et al., 2002; Chen et al., 2006), and for these two taxa, ITS diversity was comparable with *Microcystis*. However, *Synechococcus* and *Prochlorococcus* have presented a genetic structure clearly more pronounced when compared with *Microcystis* populations (Van Gremberghe et al., 2011).

Although the role of environmental selection on the distribution of several cyanobacterial taxa and habitats is well known, some factors must be taken into account. First, the spatial scale is an important factor that must be considered. Increasing environmental heterogeneity with the area along with the specificities of taxa in different habitats is the most common

explanation for taxa–area patterns (Rosenzweig, 1995); thus, it is expected that environmental selection to be stronger at finer spatial scales than at broader ones. Moreover, this is certainly a taxon-dependent pattern. For example, in an environment where increasing the area leads to an increased environmental variation, the distribution of groups with greater environmental tolerance would tend to be less dependent on spatial scale and vice versa. In addition, this relationship can be found not only among species, but also among populations of the same taxon with different habitat preferences, or ecotypes—a possible approach to be explored in future studies with other cyanobacteria taxa, mainly species that were not yet, or very little, explored.

The second issue to be taken into account is the taxonomic resolution adopted in the study. As mentioned earlier, when microbial taxa are defined from molecular approaches and classified into operational taxonomic units (OTUs), they are defined grossly through similarity in the sequence of one or more regions of the genome. Thus, since habitats are defined as a particular combination of resources and conditions necessary for a particular taxon (Tiedje, 1993), turnover habitat estimates are sensitive to the taxonomic definition, and thus, some biogeographic patterns of microorganisms may be more detectable at fine resolutions (detecting more compositional variation) than at the coarsest resolutions (Hanson et al., 2012). For example, in a scenario where "all cyanobacteria" were defined as a single taxon, one would observe a cosmopolitan distribution group with an enormous niche amplitude, and the influence of environmental selection would not be detectable. Horner-Devine et al. (2004) described taxa–area relationships for nonphotosynthetic bacteria from salt marsh sediments using different OTU definitions (95, 97 and 99% 16S rDNA sequence similarity) at scales from centimeters to hundreds of meters. This study showed that the taxa varied in the space mainly due to the environmental heterogeneity, but the turnover rate of the taxa was dependent on the bacterial lineage and the taxonomic resolution adopted: the turnover was higher with the increase of the taxonomic resolution. That is to say that finer taxonomic resolutions (e.g., 99% of sequence similarity) actually tend to detect greater compositional variation and consequently have greater power of environmental selection detection.

Regarding Cyanobacteria, a study analyzing the spatial variation of *Synechococcus* marine populations (Mazard et al., 2012) showed that in all cutoff values (88, 91, 94, 97 and 99% of similarity of multilocus sequences) the environmental factors showed a correlation with the distribution of the populations. However, the OTU definition using the cutoff value of 94% provided the best separation of the OTUs in relation to the sampled sites and the environmental parameters and, therefore, the best resolution for detecting possible ecotypes. Similarly, Martiny et al. (2009) have showed that *Prochlorococcus* distribution was dependent on the degree of sequence identity used to define a taxon (using the 16S-23SrRNA ITS region): light correlates with broad-scale diversity (90% cutoff), whereas temperature with intermediate scale (95% cutoff). These approaches not only identifies ecological differences at the population level, but also allows the analysis of the biogeographic distribution of ecotypes as a function of environmental variation and evolutionary processes, an feasible approach to be adopted in future studies with other species of cyanobacteria from many other ecosystems.

Finally, it is important to mention that genetic diversity and morphological diversity do not automatically imply the existence of ecotypes (or even different species). One case that may be mentioned is the cyanobacterium *M. aeruginosa*. Although on the one hand a high level of genetic diversity in a high number of genotypes was detected in the genus (Neilan et al., 1995; Kondo et al., 2000; Bittencourt-Oliveira et al., 2001; Wilson et al., 2005; El Herry et al., 2008; Yoshida et al., 2008; Tanabe et al., 2009; Fathalli et al., 2011; Gaevsky et al., 2011), on the other hand a number of morphospecies previously described (based on colony morphology) are not supported by molecular data forming a clade of nearly identical 16S rDNA sequences (Lepère et al., 2000; Litvaitis, 2002). Based on this extremely low 16S sequence divergence, along with DNA-DNA hybridisation data, Otsuka et al. (2001) suggested, under the rules of the Bacteriological Code, merging all morphospecies into a single species. This example shows how the concatenated sequencing of several regions of the genome is important so that issues tangible to the ecological, evolution, and obviously taxonomy, are fully understood.

Historical processes (dispersion, past environmental selection, and drift)

In this section, we discuss the first statement of the Baas-Becking hypothesis, *everything is everywhere*, which implies that microorganisms have such a great dispersion capacity so as to quickly remove the effects of past processes. Historical processes that may influence the current distribution of organisms include dispersal, past environmental selection, and drift, which may lead to genetic divergence between populations and compositional variation between communities (Martiny et al., 2006). One of the main arguments behind the 'everything is everywhere' is that the small size, large population size, and consequently the high abundance of propagules increase the dispersion rate to levels where the dispersal limitation essentially does not exist. The high dispersal rate increases the similarity in the composition of communities and decreases rates of intra- and interpopulation differentiation through increased gene flow, in the case of cyanobacteria and other prokaryotes, through horizontal gene transfer (HGT) (Martiny et al., 2006; Hanson et al., 2012).

One commonly used approach to assess the role of the dispersal limitation in structuring biological communities is through distance–decay relationship: how communities become more dissimilar as the distance between them increases (neglecting the effect of environmental variation on space) (Nekola & White, 1999; Morlon et al., 2008). Thus, the effect of geographic distance should be relatively weak in habitats where the dispersal rate is high and vice versa. Hillebrand et al. (2001) were one of the first to record this relation for microbial taxa. This study showed that in all taxonomic groups analyzed (diatoms, ciliate, corals, and polychaetes), the species similarity declined significantly with distance, being one of the first evidence of dispersal limitation for microorganisms, which contradicts the classical hypothesis about the cosmopolitan dispersion of microorganisms.

Isolated and extreme environments (i.e., island-like habitats) can act as barriers to gene flow, lead to the isolation of microbial groups—and consequently to genetic divergence, and thus facilitate speciation processes. A study based on temporal phylogenetic approach calibrated using microfossil data from the extremophile cyanobacteria *Chroococcidiopsis* (Bahl et al., 2011) from cold and hot deserts showed that there was no relation between the genetic differentiation of the lineages (based on 16S-ITS-23S rRNA) of this taxon and the geographic distance, nor on a global scale or for each phylogenetically defined cluster. However, the common ancestry time of the lineages precedes the estimates for contemporary aridity in the desert regions where this taxon occurs, indicating that the distribution of *Chroococcidiopsis* was, at least in part, limited by barriers and/or invasive colonization. Another global-scale study with *Synechococcus* from hot springs (Papke et al., 2003) showed a negative correlation between geographic distance and genetic similarity (based on 16S-ITS-23S rRNA) among the lineages, suggesting that the nonrandom and noncosmopolitan distribution of *Synechococcus* populations is influenced, at least in part, by geographic isolation and dispersal limitation. Similarly, phylogeographic patterns of thermophilic cyanobacteria *Mastigocladus laminosus* Cohn ex Kirchner from thermal areas show a significant and positive correlation between genetic differentiation (based on 16S rRNA and nitrogen metabolism loci) and geographic distance, providing evidence for this species of a distribution pattern influenced by geographic isolation (Miller et al., 2007).

Although dispersal limitation seems to be an important factor in the distribution of some cyanobacterial groups, as shown above, other groups appear to have broad dispersal abilities and (sub)cosmopolitan distributions. A study in Jordanian hot springs (Ionescu et al., 2010), for instance, showed that some cyanobacterial isolates presented high similarity (> 99% 16S rRNA) with others from hot springs of other regions of the globe. Similarly, the aforementioned study by Jungblut et al. (2010) showed that many ribotypes from Arctic showed > 99% similarity (16S rRNA) with Antarctica and Alps sequences. Among these, further, an Arctic sequence showed 99.8% similarity to the sequence of *Leptolyngbya antarctica* (West & G.S.West) Anagnostidis & Komárek sequenced from Antarctica, indicating a high dispersion capacity for this species and thus a subcosmopolitan distribution pattern. However, as will be discussed below, these subcosmopolitan distributions records have used taxon definitions based on the 16S rRNA gene sequence similarity, a very conservative taxonomic definition.

Among the examples of global dispersion, the best-known example is *Cylindrospermopsis raciborskii*.

This species is one of the most notorious cylindrospermopsin (CYN) producers that can be found in freshwater habitats in the temperate, tropical, and subtropical regions of the world (Moreira et al., 2011). It is known that to make a definite determination of the native range of microbial species is extremely difficult: *C. raciborskii* was found for the first time in 1887 in the Nile, reported as *C. kaufmannii* (Schmidle) Huber-Pestalozzi, (Wołoszyńska, 1912); however, its *Locus typicus* is, indeed, the Rava Demangan pond in Java, Indonesia (Wołoszyńska, 1912). *C. raciborskii* expanded rapidly to Europe in the last century and is considered an invasive alien species of the temperate zone (Padisák, 1997).

Phylogeographic studies have showed that populations of *C. raciborskii* are geographically grouped. Neilan et al. (2003) based on 16S rRNA and cyanobacterium-specific short tandem repeat sequence (HIP1) clustered: (1) strains from the USA and Brazil; (2) European strains (Germany, Hungary, and Portugal); and (3) Australia strains. Gugger et al. (2005) based on 16S–23S internally transcribed spacer (ITS1) revealed the same continental cluster distribution and suggested that the current expansion of *C. raciborskii* in Europe—and in Central and North Americas—did not result from recent invasion and colonization by African or Australian strains (Padisák, 1997), but rather represent local strains that maintained "cryptic" populations over time and only recently proliferated due to climate change and variations in other environmental conditions (Padisák et al. 2016). Also, Moreira et al. (2012) based on multilocus sequences recently showed that *C. raciborskii* strains grouped into three well-supported distinct clusters: (1) European, (2) African/American, and (3) Asian/Australian, and also suggested the recent invasion of *C. raciborskii* in Portuguese and other European temperate environments.

C. raciborskii has been probably the only cyanobacterial species for which dispersal routes could be reconstructed and the speed of the dispersal could be estimated: it was estimated that less than a century was needed to colonize appropriate habitats all over the world (Padisák et al., 2016). The successful dispersion of *C. raciborskii* was largely attributed to its ability to tolerate travel along river courses (Padisák, 1997). Moreover, Piccini et al. (2011) proposed that phenotypic and genetic variability of *C. raciborskii* populations is linked to the existence of different ecotypes success of which is subject to the local environmental conditions. It is also speculated that unique physiological traits of *C. raciborskii* enable their proliferation in newly colonized ecosystems, currently exposed to greater environmental and temperature disturbances (Padisák et al., 2016). Further considerations about the invasive potential of *C. raciborskii* and the possible traits related to its invasiveness can be seen in the section: "Invasions and Global Climate Change".

Phylogeographic studies with other cyanobacterial taxa also show how historical processes, such as dispersal limitation, adaptive radiation and allopatric speciation, can affect the global distributions of populations (Table 2). Another example that can be mentioned is the bloom-forming and nitrogen fixing filamentous cyanobacterium *Dolichospermum (Anabaena) circinalis* (Rabenhorst ex Bornet & Flahault) P.Wacklin, L.Hoffmann & J.Komárek. Worldwide blooms of *D. circinalis* are well known due to their production of neurotoxins as anatoxin-a and paralytic shellfish poisons (PSPs) (Padisák et al., 2016). Beltran & Neilan (2000) identified a geographic segregation of neurotoxin production in this cyanobacterium: American and European isolates of *D. circinalis* produce only anatoxin-a, while Australian isolates produce exclusively PSPs. Moreover, the phylogenetic structure of *D. circinalis* (based on 16S rRNA) suggested a monophyletic group with worldwide distribution, and the PSP- and non-PSP-producing *D. circinalis* formed two distinct 16S rRNA gene clusters (Beltran & Neilan, 2000). Although the phylogeographic structure of this cyanobacterium can not yet be fully understood, these results may suggest a truly (sub)-cosmopolitan distribution pattern followed by local environmental adaptations.

Restricted and/or endemic distributions are interesting in biogeography because a combination of factors is required to emerge them, such as geographic isolation, temporal continuity for local adaptations to accumulate, and mechanisms to reduce the intensity of HGT (Souza et al., 2008). Overall, endemism can have two different kinds of origin: the most pure form of endemism is when a species evolves at a certain location and remains exclusive to that location; and the so-called relict endemism occurs as a result of habitat fragmentation or destruction and a subsequent extinction from all localities except one (Padisák et al., 2016). Regarding cyanobacteria, some examples can

be mentioned: *Aphanizomenon manguinii* Bourrelly and *Trichormus subtropicus* (N.L. Gardner) Komárek & Anagnostidis, so far been recorded only on several islands in the Caribbean region (Komárek, 1985). Also many recently described species of *Cylindrospermopsis* which have so far been recorded only in Central America: *C. acuminatocrispa* Couté & M.Bouvy in a reservoir in NE Brazil (Couté & Bouvy, 2004), *C. catemaco* Komárková-Legnerová & R.Tavera in Lake Catemaco, Mexico (Komárková-Legnerová & Tavera, 1996) and *C. taverae* Komárek & Komárková-Legnerová in Central Mexico (Komárek & Komárková-Legnerová, 2002). And also a newly described species from Europe: *C. sinuosa* Couté, M.Leitão & H.Sarmento (Couté et al., 2004).

Polar regions are ideal locations for evaluating microbial endemism, since they contain parallel environments separated by large geographic distances and potential barriers to dispersal (Staley & Gosink, 1999), and indeed many possibly endemic cyanobacteria from Antarctica have been identified already (Taton et al., 2006; Comte et al., 2007; Jungblut et al., 2010; Michaud et al. 2012) (Table 1). In hot springs, another island-like habitat, distinct cyanobacterial populations were also characterized as possibly endemic (Papke et al., 2003; Sompong et al., 2005). Despite the importance of knowing endemic distributions, however, it is obvious that the detection of microbial endemism has some difficulties: the relation between the detection of endemism and the taxonomic resolution (as will be discussed below); the difficulty of confirming an endemic distribution because many cyanobacteria species (as well as other microorganisms) can inhabit an aquatic ecosystem unnoticed, since it may remain at a rather low biomass concentration and it does not form a conspicuous fraction of the community (Sukenik et al., 2012); and finally the difficulty of distinguishing whether a present taxon is in fact an active member of the community or a dormant transient (Curtis et al., 2002; Hanson et al., 2012). In addition, there several species that, for a long time, have been known only from the type locality (local endemics), which cannot be considered as *real endemics* as long as more surveys in the same habitat-types in other continents are missing (Padisák et al. 2016).

As for environmental selection, the influence of historical processes on the current distribution of microorganisms is dependent on the spatial scale and

taxonomic resolution adopted in the study. Here, dispersion capacity is expected to decrease with increasing distance. One study with the archaeal *Sulfolobus* (Whitaker et al., 2003) have shown this relationship, in which in spatial scales ranging from meters to tens of thousands of kilometers, the magnitude of the dispersion rate is in fact associated with the spatial scale (migration is greater between closer sites). Again, it is clear that this relationship is taxon dependent, since different taxonomic groups have different rates of dispersion and/or establishment success, and more or less capacity to cover long distances.

Regarding taxonomic resolution, both dispersion and drift (including here speciation and extinction) depends on the size of the populations, which in turn will depend on the definition of species adopted. Again, using the definition of a taxon as "all cyanobacteria", for example, would result in a large estimate of population size, high potential for dispersion, and a high probability of cosmopolitanism, and thus the influence of historical processes would be completely neglected. This relationship has already been evidenced in a study with marine populations of *Prochlorococcus* (Martiny et al., 2009), in which the distribution of the populations was correlated with the dispersal rate only in the finer taxonomic resolution examined (99.5% sequence similarity using the 16S–23S ITS region). This is a possible approach to be tested in future researches with other cyanobacterial taxonomic groups.

Finally, the relation between the detection of endemism and the taxonomic resolution is obvious. On the one hand, studies using a wide range of molecular techniques to evaluate spatial patterns of prokaryotes, such as 16S rDNA sequencing and DNA/DNA pair hybridization, indeed suggest that genera of prokaryotes are widely distributed (e.g., Hagstrom et al., 2000; Brandao et al., 2002; Zwart et al., 2002; Hedlund & Staley 2004). In addition, cosmopolitan distributions have already been recorded using a taxonomy definition based on the 16S rRNA gene (e.g., Garcia-Pichel et al., 1996; Ionescu et al., 2010; Jungblut et al., 2010). Since 1% divergence in the 16S rRNA gene being equal to isolation or reduced genetic exchange for < 10 million years (Jungblut et al., 2010), this gene is highly conserved and thought to underestimate the number of endemic species in a given habitat (Cho & Tiedje, 2000). On the other hand,

when methods that offer a fine resolution are employed, bacteria appear to have more restricted and endemic distributions (e.g., Cho & Tiedje, 2000; Whitaker et al., 2003). This same pattern occurs in studies with cyanobacteria, where endemism and restricted distributions (suggesting low dispersion capacity and/or high niche specificity) are more detected at fine taxonomic resolutions than coarser (e.g., Papke et al., 2003; Miller et al., 2007; Mazard et al., 2012).

Invasions and global climate change

The entry, establishment, and spread of nonnative species to a new ecosystem, is frequently described as biological invasion (Vitousek et al., 1997; Ricciardi & Cohen, 2007). Biological invasion is considered as an extension of normal colonization processes such as succession (Elton, 1958), and it was proposed that the term *invasive species* will be restricted to describe nonnative species that expanded their geographic range, became abundant and have environmental and economic impact (Colautti & Macisaac, 2004). Invasions also may threaten global biodiversity by altering the structure and function of ecosystems and disrupting key biological interactions (Traveset & Richardson, 2006). Indeed, when invading new areas, phytoplankton species (including cyanobacteria) are able to cause irreversible environmental changes by outcompeting native species, changing food-web structures (Dufour et al., 2006), or reduce diversity (Borics et al., 2000, 2012). Moreover, biological invasions are important in biogeography since invasion involve dispersal ability, environmental adaptation, unique physiological traits (like dormant stages as dispersal units) and ecological plasticity.

The invasion of free-living microorganisms to new aquatic habitats is rather cryptic and difficult to detect therefore invasions of these "invisible invaders" have been rarely reported (Litchman, 2010). In that sense, algae and cyanobacteria are exceptions as they have visible characteristic of spectral signature and microscopic morphological features (Sukenik et al., 2012). This property partly contributed to the increased number of records on invasion of cyanobacteria taxa, such as *C. raciborskii* (Padisák, 1997; Dyble et al., 2002; Wiedner et al., 2007; Vidal & Kruk, 2008; Sukenik et al., 2012; Wilk-Woźniak et al., 2016),

Raphidiopsis mediterranea Skuja (Wilk-Woźniak et al., 2016), *M. aeruginosa* (Moreira et al., 2014), and some species of the genus *Aphanizomenon* (Sukenik et al., 2012). Sedimentary time series and large-scale monitoring records show that both the expansion and abundance of cyanobacteria has increased significantly in the last 200 years, and more rapidly in the last 70 years (Taranu et al., 2015). Among the well-studied cyanobacteria due to their invasion potential, the most important freshwater invasive cyanobacteria are the species *C. raciborskii* (already mentioned in the section on "Historical processes") and to a lesser extent *Aphanizomenon ovalisporum* Forti, which are native to tropical regions and in the last two decades have expanded to subtropical and temperate areas (Kokociński et al., 2009; Kaštovský et al., 2010; for a detailed review on the invasiveness of these two taxa see Sukenik et al., 2012).

As already mentioned, *C. raciborskii* was an originally Pantropical species and since the first comprehensive review on its distributional area and dispersal was published (Padisák, 1997), this cyanobacterium was documented in most parts of the globe (Padisák et al. 2016). According Wilk-Wozniak et al. (2016), the distribution of the records of this species suggests the following possible migration scenarios: (1) from the center of Africa toward the north of the continent; (2) from North Africa to Europe; (3) from Java to eastern Australia; (4) from Java through South Asia to Europe and (5) from Australia to Southern Africa and on to the eastern parts of North, Central and South America. Kokocinski et al. (2017) have showed that, in Europe, the recent invasion of *C. raciborskii* in the East-Central regions may be related to environmental factors, mainly temperature-related variables. Today, *C. raciborskii* is find in many areas from Europe, such as Germany (Mischke, 2001; Stuken et al., 2006), France (Briand et al., 2002; Druart & Briand, 2002; Cellamare et al., 2010), and Poland (Stefaniak & Kokocinski, 2005; Kokocinski & Soininen, 2012; Kobos et al., 2013); and others Mediterranean/subtropical regions including Portugal (Saker et al., 2004), Algeria (Bouaicha & Nasri, 2004), Italy (Mugnai et al., 2008; Barone et al., 2010), Tunisia (Fathalli et al., 2010), Egypt (Hamed, 2005; Mohamed, 2007), and Israel (Zohary & Shlichter, 2009; Alster et al., 2010). Recent expansion of the species in South America (Vidal & Kruk, 2008;

Fabre et al., 2010) and Africa (van Vuuren & Kriel, 2008) toward higher latitudes is also documented (Padisák et al. 2016). Several studies published in the literature concerns its invasiveness potential (e.g., Padisák 1997; Sukenik et al., 2012; Wilk-Woźniak et al. 2016), and part of this effort is due to the fact *C. raciborskii* is a potentially toxic and bloom-forming cyanobacterium. Australian strains, for example, are known to produce cylindrospermopsin, and Brazilian strains have been reported to produce paralytic shellfish poisoning toxins (Neilan et al., 2003).

Since the invasion must be initiated with dispersion to new zones (by aeolian transport, migrating animals, and also facilitated by human activities) and the subsequent establishment to the new environment, the invader needs a set of traits that support its establishment and proliferation (Sukenik et al., 2012). Regarding *C. raciborskii*, and also other Nostocales cyanobacteria, can be mentioned: the ability to form dormant cells (akinetes) that may survive long and extreme dispersion routes and survive on unfavorable conditions; and the ability to fix atmospheric nitrogen in the absence of combined inorganic sources, thus extending the spectrum of ecosystems to which they can invade (Sukenik et al., 2012). This species may also utilize other limiting resources, such as phosphorus, more efficiently than other cyanobacteria due to high affinity and P storage capacity (Isvánovics et al., 2000; Wu et al., 2012). Moreover, an important feature of *Cylindrospermopsis* is its wide thermal tolerance (Briand et al., 2004), which is essential to maintain the populations during cold winters. Padisák (1997), for instance, have reported that akinetes of *C. raciborskii* germinate at temperatures < 24°C. Finally, allelopathy (ability to synthesize allelo-chemicals that inhibit other phytoplankton species or deter and reduce grazing) was suggested as a beneficial trait of *C. raciborskii* that contributes to its stable dominance and geographic expansion (Fastner et al., 2007; Figueredo et al., 2007; Paerl et al., 2011).

Besides *C. raciborskii*, some other potentially invasive species of cyanobacteria are mentioned in the literature. For instance, dispersal of halophilic species in temperate waters has been facilitated by winter de-icing of roads and improper treatment of industrial sewage (Kaštovský et al., 2010). In that sense, it can be mentioned the cyanobacterium *Cuspidothrix issatschenkoi* (Usachev) P.Rajaniemi, Komárek, R.Willame, P. Hrouzek, K.Kastovská,

L.Hoffmann & K.Sivonen (Padisák et al., 2016), whose expansion in the twentieth century might be enhanced by gradual adaptation to typical freshwater environments and the ongoing climate warming (Kaštovský et al., 2010). Also, *Planktothrix rubescens* is another cyanobacterium whose invasive potential has been described in the literature (Kaštovský et al., 2010; Padisák et al., 2016). This species had its original distribution area covering southern central Norway and the western alpine area, especially large lakes in Switzerland, Austria Italy, Germany, Slovenia, and France (e.g., Barco et al., 2004; Jann-Para et al., 2004; Jacquet et al., 2005; Legnani et al., 2005; Ernst et al., 2009). In addition to appears to proliferate within its original area (Jacquet et al., 2005), increasing number of reports provide evidence for its dispersal both southward and eastward to Spain (Almodóvar et al., 2004; Barco et al., 2004), Portugal (Paulino et al., 2009), Central Italy (Messineo et al., 2006), Sicily (Naselli-Flores et al., 2007; Naselli-Flores, 2014), Greece (Vareli et al., 2009), Turkey (Albay et al., 2003; Akcaalan et al., 2007), Poland (Krupa & Czernas, 2003; Lenard, 2009), and Hungary (Vasas et al., 2014) (Padisák et al. 2016).

One can not fail to mention the role of global climate change in cyanobacterial invasion patterns. This is because global warming leads to worldwide proliferation of cyanobacterial species, thus increasing its invasiveness potential, and consequently increasing blooms events. In addition to local environmental changes that can potentially increase cyanobacteria proliferation (e.g., nutrient overenrichment of waters), climate change is a potent catalyst for the further expansion of cyanobacterial blooms (Paerl & Huisman, 2008, 2009; Häder & Gao, 2015). Rising temperatures favor cyanobacteria in several ways, thus increasing its potential for invasiveness: (1) cyanobacteria generally grow better at higher temperatures (often above 25°C), giving a competitive advantage at elevated temperatures (Elliott et al., 2006; Jöhnk et al., 2008); (2) global warming causes lakes to stratify earlier in spring and de-stratify later in autumn, which lengthens optimal growth periods; and finally, (3) global warming affects patterns of precipitation and drought, for example, more intense precipitation will increase surface and groundwater nutrient discharge into water bodies (Paerl & Huisman, 2008).

Harmful blooms of toxic cyanobacteria are of particular interest and concern because of their economic and health consequences (Rastogi et al., 2015). Harmful blooms due to excessive growth of certain cyanobacteria followed by the production of toxic compounds have been reported in many eutrophic to hypertrophic lakes, ponds, and rivers throughout the world (Rastogi et al., 2015) Many of these bloom events, for instance, are of toxic *Microcystis* species and strains that proliferate under current environmental alterations, including nutrient enrichment, global warming, and regional hydrologic changes (Paerl & Paul, 2012). Microcystin is among the most commonly occurring toxin produced by cyanobacteria in natural waters (Babica et al., 2006; Rastogi et al., 2015), and can cause liver complications and damage to the nervous system if ingested (Bláha et al., 2009). Moreover, it has been suggested that UV-B radiation may significantly influence strain composition of cyanobacterial blooms in favor of microcystin (MC) producers (Ding et al., 2013).

Another cyanobacterium potentially harmful-bloom forming is the already mentioned *C. raciborskii*. In a modeling effort, for instance, Mehnert et al. (2010) have demonstrated that under a scenario of climate change with an increase of 4°C in the water temperature, *C. raciborskii* would outcompete a native species (*Aphanizomenon gracile* Lemmermann). Also, temperature-dependent release of cylindrospermopsin and microcystin has already been reported for *A. ovalisporum* (Cirés et al., 2014), *Planktothrix agardhii* (Walls et al., 2018) and *Microcystis* (Dziallas & Grossart, 2011), implicating management complications associated with global change scenarios. However, it is worth to mention that not all harmful blooms are associated with an invasion process, since many cyanobacterial species are of broad geographic distribution and rapidly respond to current environmental changes. Furthermore, although temperature (and global warming) are recognized as important factors leading to the proliferation of cyanobacteria, the exact mechanisms and the role of environmental factors regulating harmful blooms are disputable and yet to be understood, requiring more efforts both through field data and through experiments and modeling approaches.

Concluding remarks and future research perspectives

The central and global importance of microorganisms in the natural ecosystems throughout the world is obvious, however, despite the increase of studies and data, the application of ecological and evolutionary theories in microbial systems is still very limited. From the body of evidence collected by that time, it is known that a variety of nonmutually exclusive factors influence the distribution of microbial diversity on the planet, such as environmental selection (e.g., Mazard et al., 2012), allopatric speciation (e.g., Dvořák et al., 2012), and dispersal limitation (e.g., Miller et al., 2007), which during a long time was assumed did not exist for the microorganisms (Baas-Becking, 1934; Finlay, 2002; Fenchel & Finlay, 2004). Regarding cyanobacteria, there is also an increase of interest in phylogeographic and biogeographic studies, from approaches that go beyond ecological and taxonomic traditional studies from a solely microscopic approach. However, the studies still comprise a very small variety of habitats and taxonomic groups explored (Tables 1 and 2). Due to the highly diverse character of these group, from unicellular to multicellular organisms with differentiated cells (heterocyst and akinetes), with free-living and associated/symbiotic life forms, and present in the most diverse habitats of the Earth, interesting perspectives for future biogeographic studies emerge.

As expected from the Baas-Becking hypothesis, environmental selection is indeed found to have some influence on cyanobacterial distribution patterns of various taxonomic groups and habitats (Tables 1 and 2). The studies reported here show that both in global scales (e.g., Zwirglmaier et al., 2008) and at local scales (e.g., Chamberlain et al., 2014), environmental characteristics influence, at least in some degree, the distribution of cyanobacteria. The key question here is how distinct taxa, and how distinct taxonomic resolutions adopted to define a "taxon", respond to environmental variation. We think, therefore, that future biogeographic studies within this section will benefit from exploring issues such as: (i) what is the ecological relevance of different levels of taxonomic resolution adopted for a given taxon?; (ii) what level of taxonomic resolution is required for the detection of ecotypes of a given species and how important are the environmental variables that potentially structure the

distribution of ecotypes?; (iii) how do different taxonomic and trait-based groups respond to environmental variation?; (iv) how the cyanobacterial traits are distributed and responding to environmental variation?

On the influence of historical processes, recent studies with contradictory evidences about microbial cosmopolitism have been debating this issue, including studies with cyanobacteria taxa (Table 2). Thanks to previous studies, it is clear that dispersal capacity is dependent on several factors, such as the traits and dispersion strategies of give taxon may influence your establishment success (Hanson et al., 2012 and cited references). Akinetes-forming cyanobacteria, for instance, may have a greater dispersion capacity than those that do not form these structures because it is more likely to remain viable until arrival in a favorable habitat (in addition to decreasing the likelihood of extinction in front to environmental fluctuations) (see discussion on *C. raciborskii* in the sections above). In addition, the type of habitat may have some influence on the microbial dispersion. For example, taxa from sediment may have a lower dispersion capacity relative to taxa from surface soil in the same ecosystem or geographic area.

In the context of historical processes, therefore, interesting questions still need to be explored in the future, such as: (i) how different taxonomic groups (defined at different levels of taxonomic resolution) and trait-based present patterns of dispersion and gene flow? (ii) in fluid/continuous habitats (e.g., lakes, oceans) the rate of dispersion is greater than in island-like/poorly flowing habitats (e.g., periphyton, soil crusts)?; (iii) what is the role of population isolation, HGT and genetic drift in cyanobacterial distribution patterns at large spatial scales and at fine spatial scales (using target molecular markers for each purpose)?; (iv) what are the dispersive routes of different taxa and how do they vary over time? (that is, to apply molecular clocks in order to put the spatial distribution of different cyanobacteria taxa into a temporal framework).

Finally, to answer all these questions, in addition to studies with field data, both manipulative experimental tests and temporal studies are needed. Experimental manipulations have the potential to be useful tools for understanding how environmental and spatial factors influence the distribution of microbial taxa because microorganisms provide much better controlled and more flexible experimental systems for testing ecological theory than larger organisms (Bell, 2010). For instance, one experimental study has identified a specific temporal window during which the effects of dispersal limitation were apparent, although a subtle environmental variation operating over time scales of a few days can quickly overcome this dispersal limitation (Bell, 2010). Also, another experimental study showed that the slope of the taxa–area relationship for natural bacterial communities inhabiting small aquatic islands is comparable to that found for larger organisms (Bell et al., 2005). These approaches can provide important insights into biogeography of cyanobacteria, providing the opportunity of analyzing dispersion, HGT, and environmental selection more precisely: for instance, testing taxa–area and distance–decay relationships, correlations among abundance, genetic diversity, and ecotypes diversification, and the comparison of these patterns among different species and clades of cyanobacteria on controlled environmental conditions.

Conclusions

Among prokaryotic organisms, cyanobacteria are one of the most morpho-physiologically distinct groups (from unicellular to multicellular life forms; with or without differentiated cells; with toxic, invasive, and bloom-forming capacities; etc.), and this feature provides interesting approaches for biogeographic studies that are still little explored. In an overview, biogeography of cyanobacteria is still in its infancy, and generalizations cannot yet be made. On the one hand, considered (sub)cosmopolitan species may actually represent ecotypes with restricted distributions; on the other hand, species with restricted or endemic distributions may actually be the result of an underestimation of occurrence due to insufficient sampling effort. Due to the ecological, sanitary, and economic importance, bloom-forming and invasive toxic species are still the most studied, and of which there are more data available, both ecological and genomic, in the literature. Thus, making efforts to know and map the real diversity of cyanobacteria in the most diverse ecosystems is the first step to leverage the study of biogeography of this group. The exploration of little-known geographic areas (e.g., subtropical environments) and habitats (e.g., terrestrial,

microbial mats), as well as sampling and sequencing genomes from cyanobacteria of lesser-known taxa, is very much needed to improve our understanding on the biogeography of cyanobacteria.

So far, the fact that there are some cyanobacteria species with broad distributions and others with possible endemic distributions implies the nonuniformity of the responses of different taxa to ecological/evolutionary processes. To what extent these distribution patterns are dependent on species concept, level of taxonomic resolution, spatial and environmental scales, and the biases of the molecular methodologies applied in the studies, are key issues to be explored in future studies. We suggest that to answer these questions adequately, it is necessary to use multiple taxonomic definitions based on a variety of genetic markers (and biochemical and morphological characteristics, more easily accessible for cyanobacteria), and subsequent testing of hypothesis in the light of ecological and evolutionary theories. It should also be noted that taxonomic identification based on molecular methods, although has higher detectability of variation in biodiversity, actually provides data for the investigation of biogeographic patterns of microbial genes, not whole organisms. Therefore, another possible approach is to compare biogeographic patterns of cyanobacterial genes with whole genomes (already available for some cyanobacterial species) and microscopic-based definition, by analyzing how distribution patterns depend on the definitions of cyanobacterial species adopted.

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