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Review

Underestimated cyanobacterial diversity: trends and perspectives of research in tropical environments

Petr Dvořák[1], Petr Hašler[1], Dale A. Casamatta[2*] & Aloisie Poulíčková[1]

[1] *Department of Botany, Faculty of Science, Palacký University in Olomouc, Šlechtelů 27, CZ–783 71 Olomouc, Czech Republic*
[2] *University of North Florida, Department of Biology, University of North Florida, Jacksonville, Florida, USA;*
[*]Corresponding author: dcasamat@unf.edu

Abstract: Cyanobacteria are photo–oxygenic prokaryotes present in nearly all ecosystems, where they are important in global oxygen, carbon, and nitrogen cycles. They are often recognized as the harbingers of eutrophication in freshwater systems and are increasingly being noted as nuisance species in marine ecosystems such as coral reefs. In recent years, cyanobacteria have been intensely studied due to their toxicity, harmful bloom formation, and because their distribution and abundance are expected to increase with climate change. Nevertheless, for all of their importance, many gaps in our knowledge of cyanobacteria remain: the distribution, dispersal, and biogeography of these microorganisms are still not understood. Until 1994 little attention was paid to tropical cyanobacteria and their diversity, despite some harmful invasive species having their putative origins in tropical habitats. However, more practiced articulation and research has recently uncovered previously undescribed biodiversity, and in turn changed our knowledge of the evolutionary relationships within the Cyanobacteria. The purpose of this paper is to describe the challenges of working with the cyanobacteria and to review what we know of them from tropical habitats.

Key words: cyanobacteria, diversity, tropical environment, biogeography, new genera

INTRODUCTION

Cyanobacteria are a diverse group of photo–oxygenic bacteria that contain chlorophyll *a* and are found in myriad habitats. Amongst the oldest known bacterial lineages, fossil records date back to 3.5 BYA (Schopf 2000). The most recent study based on a combination of genetics and fossil evidence suggest their origin to mid–Archean, long before the Great Oxidation Event (2.5–2.3 Ga), with multicellularity evolving towards the end of the Archean (Schirrmeister et al. 2015). The earliest lineages of cyanobacteria likely inhabited the benthos of freshwater ecosystems (Uyeda et al. 2016). Cyanobacteria are common components of nearly all ecosystems and range from oceans, freshwaters, soils and extreme habitats (for review see Whitton & Potts 2000; Warren–Rhodes et al. 2006). They are also important members of symbiotic relationships with lichens, plants, and other phototrophs (e.g., Rai et al. 2002; Usher et al. 2007; Villanueva et al. 2019). Not merely relegated to aquatic habitats, cyanobacteria are also common terrestrial pioneers and form the basis of cryptogamic crusts (Johansen 1993; Büdel et al. 2002; Nguyen et al. 2017). Cyanobacteria are also important global ecosystem level engineers and their total biomass is estimated at ca. 3.0×10^{14} g C (Garcia–Pichel et al. 2003), and may constitute up to 50% of oceanic primary productivity (Falkowski 2012). Although diatoms have been generally considered the standard algal bioindicators, routine cyanobacterial monitoring, especially in freshwater habitats, is increasing (Mateo et al. 2015; Monteguardo 2016). Non–toxic cyanobacteria are sources of food for many organisms, forming the base of the food web in aquatic ecosystems (Nweze 2009). Moreover, *Nostoc* and *Arthrospira* have been considered delicacies for centuries (Mexico, Peru, Lake Chad region of Africa and China; reviewed by Nweze 2009).

Cyanobacteria have other significant ecological roles, including global oxygen production (Kasting & Siefert 2002; Lyons et al. 2014) and carbon flux (Charpy et al. 2012). In nitrogen–limited tropical ecosystems, they may be the primary source of nitrogen fixation (Hoffmann 1999; Abed et al. 2006; Charpy et al. 2010). Marine cyanobacteria are responsible for ca. 50% of the global biological nitrogen fixation (Gruber et al. 2008). While the filamentous, planktonic genus *Trichodesmium* represents a major marine nitrogen source (Hoffmann

1999; Bergman 2001; Capone et al. 2005), small, unicellular, diazotrophic cyanobacteria (e.g., *Crocosphaera watsonii*, *Synechococcus*, *Synechocystis*) are also significant nitrogen contributors (Spiller & Shanmugam 1987; Zehr et al. 2007; Moisander et al. 2010; Saha et al. 2012), albeit with less efficiency (Paerl 2017). Although benthic cyanobacterial diversity in tropical coastal areas remains largely unexplored, their contribution to nitrogen fixation has already been documented (Abed et al. 2006; Díez et al. 2007). It has been suggested that nitrogen limitation in tropical habitats has facilitated numerous symbiotic associations with both terrestrial and marine organisms (e.g., *Geosiphon*, *Blasia*, *Azolla*, *Macrozamia*, *Gunnera*, corals, sponges; reviewed by Meeks 1998; Li 2009; Lesser et al. 2004).

In recent years, cyanobacteria have increasingly been studied for their roles in freshwater harmful algal blooms (for review see Huisman et al. 2005; Paerl & Huisman 2009; Quiblier et al. 2013) and because their distribution and abundance are expected to increase with climate change (Dvořák & Hašler 2007; Pearl & Paul 2012; Wilk–Wozniak et al. 2016), particularly global warming (Antunes et al. 2015). For example, experiments have shown that increasing temperatures lead to a shift from the dominant native species *Aphanizomenon gracile* to the invasive species *Raphidiopsis* (previously *Cylindrospermopsis) raciborskii* (Mehnert et al. 2010). However, these successional relationships are complex; for example, the coexistence of *R. raciborskii* and *Planktothrix agardhii* seems to be influenced by light intensity rather than by temperature, with the growth of shade adapted species *P. agardhii* favored by the co–occurrence of *R. raciborskii* due to its shading effect (Hašler & Poulíčková 2003; Poulíčková et al. 2004; Bonilla et al. 2016).

Studies on tropical toxic cyanobacterial blooms are sporadic and the occurrence of toxic cyanobacterial strains is likely underestimated (reviewed by Antunes et al. 2015). The frequently occurring, planktonic genera *Microcystis* (occurring in tropical Asia, Africa and Central America), *Raphidiopsis,* and *Anabaena/ Dolichospermum* (tropical Australia, America, Africa) have been recorded in tropical environments by Mowe et al. (2015). Tropical cyanobacteria are also being identified as potential competitors or pathogens of marine organisms, such as corals (e.g., black–band disease; Stanic et al. 2010; Casamatta et al. 2012). Toxins produced by cyanobacteria are even being recovered from aerial samples (Wilde et al. 2014; Breinlinger et al. 2021). Numerous secondary metabolites have been identified from freshwater and marine taxa (e.g. Bláha et al. 2009; Mazard et al. 2016). These metabolites include potent toxic compounds (Dittmann et al. 2013; Moreira et al. 2013), but also include a wide array of biologically active compounds that may be of human benefit, exhibiting anti–cancer, anti–viral, anti–bacterial, and anti–protistan properties (for review see Singh et al. 2011; Zanchett & Oliveira–Filho 2013).

Cyanobacteria were traditionally, broadly organized into four major lineages based on type of cell division and the presence of specialized cells. However, this system needs revision and no currently proposed taxonomic schemes are universally accepted (e.g., Komárek 2010, 2011, 2018; Komárek et al. 2014). Taxonomic classification is confounded by the fact that cyanobacteria fall under both the International Code of Nomenclature of algae, fungi and plants and International Code of Nomenclature of Bacteria (Oren 2011; Oren & Ventura 2017). While the most commonly employed scheme was introduced by Rippka et al. (1979) and modified by Castenholz et al. (2001), we, and most researchers now, employ the botanical approach and scheme set forth by Komárek et al. (2014).

Traditionally, cyanobacteria have been extensively studied in temperate zones due to the prevalence of researchers associated with these habitats. Since 1994, an increasing attention has been paid to tropical cyanobacteria and their diversity (Fig. 1). However, the number of all species (Fig. 2) and newly described genera (Table 1) reflect unequal effort in respect to different tropical countries. Recent evidence suggests that the cyanobacteria as a whole possess much greater molecular diversity than is evidenced in morphology (e.g. Casamatta et al. 2003; Hašler et al. 2011, 2012, 2014a,b; Sili et al. 2011; Vaccarino & Johansen 2011; Palinska et al. 2012; Dvořák et al. 2012, 2014, 2015b; Hauer et al. 2013; Komárek et al. 2013a,b; Komárková et al. 2013; Krienitz et al. 2013; Engene et al. 2018). Questions still remain as to whether true tropical taxa even exist, or if cyanobacteria are ecologically ubiquitous in permissive habitats. Explanation will need more sequence data in public databases and higher accuracy in their identification, because many sequences refer only to cyanobacterial genera, or left unresolved as "uncultured" (Dvořák et al. 2018). The purpose of this paper is to explore the state of tropical cyanobacterial diversity, ecological roles and putative evolutionary patterns. For the purposes of this paper, we define tropics as a region between subtropical high–pressure regions between 30–35 North and South latitudes (Henry 2005).

Cyanobacterial species concepts and definitions

Inherent to any discussion of biodiversity are two main questions: i) what is a species and ii) how does cryptic diversity influence our notions about diversity? While cyanobacteria are technically bacteria, they have traditionally been regarded as "algae", and are governed by both the Botanical and Bacteriological Codes of Nomenclature. Although discussions of species concepts are not new (Castenholz & Norris 2005; Oren & Garrity 2014; Palinska & Surosz 2014), cyanobacteria represent an especially problematic lineage. Komárek (2010, 2011, 2018, 2020) published critical comments on some problematic aspects of cyanobacterial species designations. The author pointed out the necessity to study both natural populations and cultivated material in order to accurately account for phenotypic plasticity (for a review of potential issues arising from such plasticity see discussions by Drouet 1968, 1973). While traditionally organized based on major morphological features (e.g., presence or absence of specialized cells, types of cell division, mechanisms of reproduction, etc.), the currently accepted metric for species delineations is analysis of 16S rRNA gene (e.g. Nübel et al. 2008; Iteman et al. 2000) similar to bacteria (Caro–Quintero & Konstantinidis 2012). Unfortunately, the 16S rRNA gene itself does not provide sufficient resolution for species level designations in cyanobacteria (Johansen & Casamatta 2005; Casamatta et al. 2005), and thus may miss critical cryptic diversity (Casamatta et al. 2003). Moreover, multiple ribosomal operons are often present in the cyanobacterial genomes. While they are almost identical in most cases, *Scytonema hyalinum* possesses two types of highly diverged operons with 7.3–9.0% of difference between them (Johansen et al. 2017).

Researchers are increasingly also employing 16S–23S ITS secondary folding structures as phylogenetically informative characters, as this region easily undergoes changes more than the conservative 16S rRNA gene. In addition, resolution on the species or infraspecific level is very high (Lukešová et al. 2009; Perkerson et al. 2011; Osorio–Santos et al. 2014) and so the ITS secondary structures represent another effective tool of modern taxonomy of cyanobacteria (e.g. Boyer et al. 2001; Casamatta et al. 2006; Siegesmund et al. 2008). To avoid the problems associated with single–gene phylogenies, multilocus and phylogenomics datasets are also being utilized (Ahlgren et al. 2012; Mazard et al. 2012; Komárek et al. 2014; Schirrmeister et al. 2015; Alvarenga et al. 2017; Mareš 2018). Another method with a sufficient resolution to recognize cryptic lineages is peptide/protein profiles (intact cell MALDI–TOF – matrix assisted laser desorption ionization–time of flight mass spectrometric analysis). While this method seems to have higher sensitivity than analysis of 16S rRNA gene, while being both cheaper and simpler then genomic analysis (Šebela et al. 2018), few researchers employ this method at present.

Current classification of cyanobacteria employs a polyphasic approach, using study of natural populations and cultures, a detailed evaluation of morphological variability, ecology of species, ultrastructure and molecular analysis (Komárek 2018, 2020). Current estimates indicate that there exist >6000 species of cyanobacteria (Nabout et al. 2013), but this estimate is highly conservative and probably will be shattered as more habitats are sampled. Further, with an advent of next generation sequencing, it has become obvious that the ITS patterns can only provide limited insights into diversity. Phylogenomic analyses (phylogenies based on a whole genome data) reveal that there appear cryptic species (taxa, ecotypes),

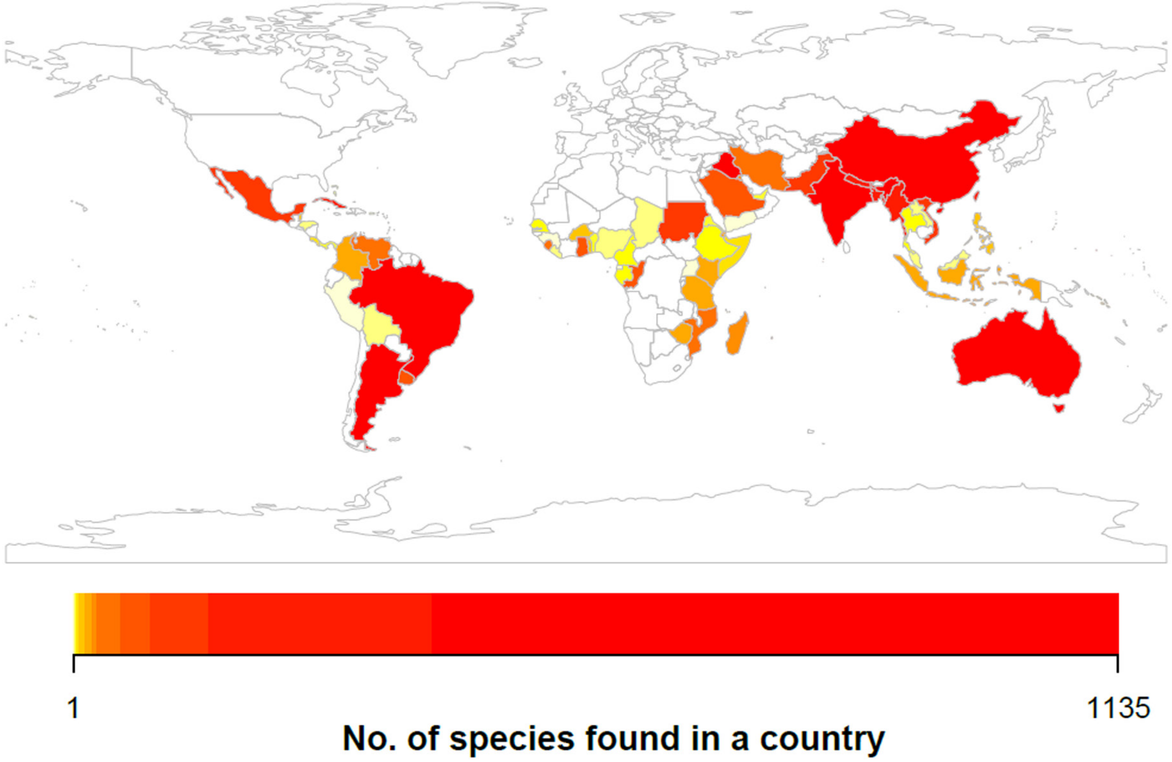

Fig. 1. Cyanobacterial diversity in the tropical countries. The color gradient represents the number of species found per country. All accession numbers from tropical countries were downloaded for the whole world from AlgaeBase (12 February 2020, https://www.algaebase.org/search/distribution/). The number of species found in a particular country was drawn using R (R Core Team 2020), package rworldmap 1.3–6 (https://cran.r–project.org/web/packages/rworldmap/index.html).

which might be identified only using whole genome data (e.g. Rocap et al. 2003). While 411,496 complete or draft genomes are available for bacteria, only 1,842 cyanobacterial draft or complete genomes are available in NCBI (22nd February 2021). Thus, cyanobacteria are still behind with data in comparison to other prokaryotes (Alvarenga et al. 2017). Dvořák et al. (2020) showed that whole–genome of cyanobacterial herbarium specimens can be sequenced. Herbarium specimens may provide a unique source of reference data for the phylogenomic analyses and taxonomic revisions.

Recent research suggests that tropical cyanobacterial biodiversity is likely extremely high. The actual elucidation of this diversity is confounded by morphological similarity with species from temperate zones and cryptic diversity, which requires the use of sensitive phylogenetic methods. Further, a dearth of specialized modern keys from the tropics leads to more difficulties. The most comprehensive key books on tropical cyanobacteria were published by Gardner (1927), Frémy (1930) and Desikachary (1959). The three recently published monographs of the Süsswasserflora von Mitteleuropa keys (Komárek & Anagnostidis 1999, 2005; Komárek 2013) are the most employed cyanobacterial keys throughout the world. Unfortunately, these books focus almost exclusively on European flora, while taxa occurring in the tropical regions are mentioned without keys to their identification. The expected occurrence of cosmopolitan species and number of tropical species in the aforementioned recent and classical monographs enable their common use as the basic source of knowledge for studying diversity of tropical cyanobacteria.

Another caveat in an identification of the tropical cyanobacteria lies in the frequent polyphyly within almost all cyanobacterial genera. For example, cosmopolitan genera such as *Phormidium*, *Leptolyngbya*, *Microcoleus*, and *Synechococcus* are composed of several lineages without common origin but with a coherent morphology. The most recent and complex review is given in Komárek et al. (2014), who proposed to call these polyphyletic conglomerates “cryptogenera”. In some cases, such morphological coherence may mask a geographical origin. For example, *Pseudanabaena galeata* frequently occurs in the plankton of fresh–water lakes in the temperate zone. Recently, a morphologically indistinguishable morphospecies has been isolated from the plankton of tropical fresh–water bodies. However, phylogenetic analyses of 16S rRNA regions has revealed the tropical morphospecies actually belong to another lineage distantly related to *P. galeata, Pinocchia polymorpha* (Dvořák et al. 2015a). In many cases, genetic differences are quite extensive. For example, two newly identified genera *Ammassolinea* (Hašler et al. 2014b) and *Jacksonvillea* (Hašler et al. 2017) found in Florida showed that they were ~10% different from other cyanobacteria 16S rRNA sequences stored at GenBank. A survey of the GenBank 16S rRNA sequences by Dvořák et al. (2018) revealed that only 21% of species stored there are correctly identified, further emphasizing potential problems arising from the cryptogenera.

Although the trend to erect new taxa is robust (see Table 1), most of the studies are based on one or two strains, perhaps leading to spurious results as additional strains are sequenced. To articulate this issue, Pietrasiak et al. (2019) studied *Myxacorys* gen. nov. from desert soil crusts. They isolated 42 strains and proposed a new genus with two new species *Myxacorys californica* and *M. chilensis* on the basis of 16S rRNA

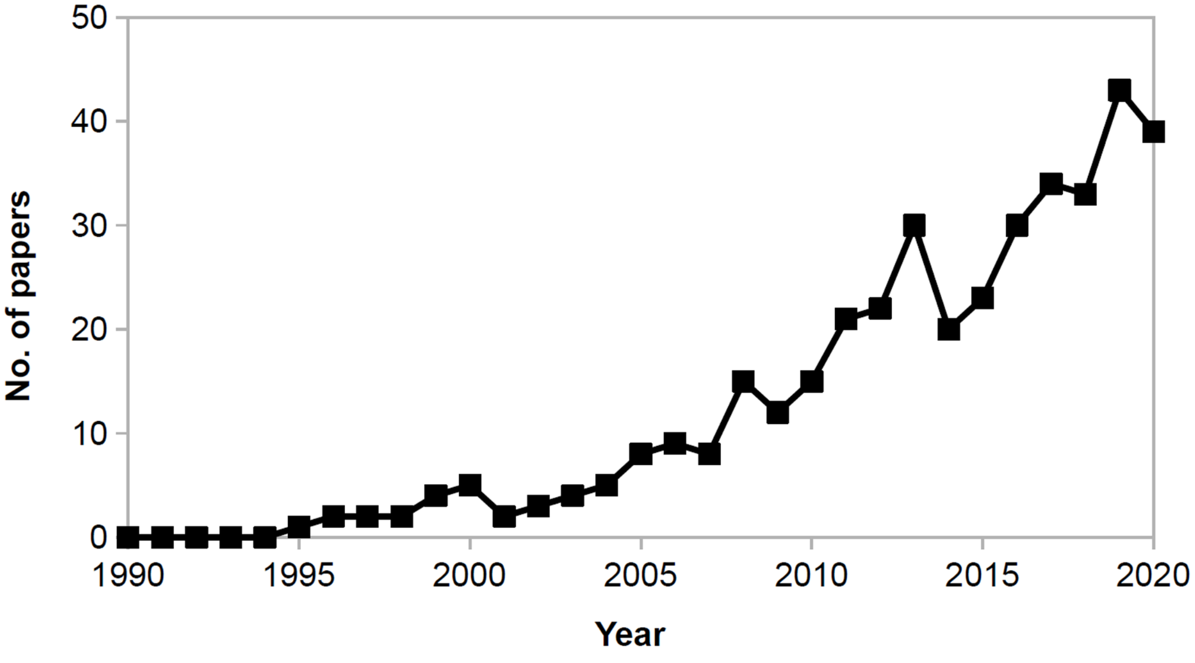

Fig. 2. Number of papers from Web of Science (to date 22 February 2021) which dealt with the tropical diversity of cyanobacteria each year employing the terms: cyanobacteria, diversity, tropics, and a particular year.

gene sequences. But they also found distinct 16S–23S ITS sequence variability within species, with three distinct lineages within *M. californica* and five within *M. chilensis*. They articulated this surprising result with the question: "what is the line between species, or, put differently, when is it justified to describe a cyanobacterial species?" (Pietrasiak et al. 2019).

Pioneer morphological studies

Little attention has been paid to tropical cyanobacteria and their diversity. The most important and comprehensive first monographs on tropical cyanobacteria were published by Frémy (1930) and Desikachary (1959), who studied diversity across Paleotropical regions. Both authors classified cyanobacteria employing a traditional botanical approach. Frémy reported 227 species of cyanobacteria from equatorial Africa, representing 57.9% of the total cyanobacterial diversity in Africa (392 species). The author distinguished three groups of species: i) cosmopolitan or species occurring across the world, ii) exclusively tropical species, and iii) those taxa which occurred only in equatorial Africa (most likely endemic species). Frémy collected cyanobacterial samples from diverse habitats, including dry rocks, wet soils and wet bark, leaves, and mosses. Aquatic habitats elicited a higher diversity of cyanobacteria. Numerous taxa were found as periphyton on submerged trees, plants, stones, etc. or free–floating, including many traditional temperate genera.

Desikachary (1959) reported 85 genera and 750 species of cyanobacteria in India and surroundings regions. Approximately 145 species were designated as cosmopolitan and 31% of species corresponded to European records. A similar situation described Komárek (1985) who recorded 45% rate of endemism from Cuba. Gardner (1927) described 216 new species of neotropical flora in the monograph New Myxophyceae from Puerto Rico, among which *Lyngbyopsis willei* (a monotypic genus) represents an endemic cyanobacterium of the Caribbean region. Floristic research from the other countries in Central America (Mexico, Belize) showed a high diversity of cyanobacteria and numerous new species or genera were found in various habitats. Historical records indicate that tropical habitats contain both autochthonous tropical flora as well as cosmopolitan species. Tropical cyanobacteria can be pantropical or restricted to narrow, geographically limited regions.

Gardner (1927) described many genera commonly encountered in temperate regions, but with high intrageneric diversity. For example, *Scytonema* included 22 species and varieties, of which the majority represents species found only in Puerto Rico. However, it must be noted that recent molecular analyses have erected new genera to encompass many of these taxa, such as *Chakia* (Komárková et al. 2013; formerly *Sc. catenulum*, *Sc. evanescens*) or *Brasilonema* (*Sc. lyngbyoides*). Similarly, the genus *Stigonema* showed a high intrageneric diversity (15 species and varieties), the majority of which have only been found in Puerto Rico (*St. hormoides* var. *constrictum*, var. *rigidum*, var. *lineare*), potentially representing new taxa.

Modern polyphasic studies

Recently, researchers have greatly expanded our knowledge of cyanobacterial diversity in tropical habitats (Table 1, Fig. 1, Fiore et al. 2007; Sant´Anna et al. 2010, 2011; Ramírez et al. 2011; Sant´Anna et al. 2011; Lemes–da–Silva et al. 2012; Jahodářová et al. 2017, 2018). The reasons for such increase can be found in general globalization – accessibility of traveling, increasing use of molecular methods, and expansion of polyphasic studies. The description of new genera in Table 1 has been achieved using a polyphasic approach supported by International Association for Cyanophyte Research (IAC) (Komárek 2011).

First, it may be argued that the prevalence of tropical cyanobacteria may be increasing in both terms of abundance and distribution. For example, migratory birds to Europe or across America can introduce tropical species such as *Raphidiopsis raciborskii*, which may be successfully established due to global climate change (Dyble et al. 2002; Mehnert et al. 2010; Sukenik et al. 2012). Cellamare et al. (2013) have pointed out that cyanobacterial dispersal along the Aquitaine region of France is due to birds migrating from Africa. In general, planktic species are expected to have wider, easier dispersion than benthic taxa (Naselli–Flores & Padisák 2016).

Second, the pioneering works examining tropical cyanobacterial diversity were based solely on light microscopy (LM) studies. However, the limited resolution of LM, coupled with simple cyanobacterial morphology, subtle apomorphies, and potentially widespread cryptic diversity represent the limitations of taxonomy in the 19th and 20th centuries (Casamatta et al. 2003; Sherwood et al. 2015; Engene et al. 2018). The lack of keys to tropical taxa led to further confusion, with many temperate taxa described from tropical areas due to an overreliance on morphological assessments. For example, Engene et al. (2011, 2012, 2013a, 2013b, 2018) focused on the ubiquitous tropical marine genus "*Lyngbya*". Using molecular, morphological, and chemotaxonomic characters, they have clearly demonstrated vast phylogenetic diversity in what has traditionally been considered a species depauperate clade. In contrast, the genus *Sphaerocavum*, which co–occurs with *Microcystis* in eutrophic Brazilian lakes, was initially described as a separate genus based on morphology (Azevedo & Sant´Anna 2003), but later phylogenetic analyses revealed this to be mere phenotypic plasticity (Rigonato et al. 2018).

One of the most–studied tropical areas is Central and Southern America. Specialists have begun to investigate freshwater, subaerophytic, and aerophytic populations of cyanobacteria from Cuba, Mexico, Belize and Brazil, which has resulted in numerous new taxa (Fig. 2, Table 1, e.g. Komárek & Hindák 1975; Montejano

Table 1. New genera described from tropical environments (2015-2020). Data based on CyanoDB http://www.cyanodb.cz/.

Genus	**References**	**Habitat**	**Taxonomic lineage**	**Area**
Aliterella	Rigonato et al. 2016	Marine	Chroococcidiopsidales	Brazil
Aliinostoc	Bagchi et al. 2017	Benthic	Nostocales	India
Alkalinema	Vieira Vaz et al. 2015	Saline wetland	Synechococcales	Brazil
Amazoninema	Genuário et al. 2020	Stream	Synechococcales	Brazil
Amphiheterocytum	Sant´Anna et al. 2019	Planktic	Nostocales	Brazil
Ancylothrix	Martins et al. 2016	Stream benthos	Oscillatoriales	Brazil
Caldora	Engene et al. 2015	Marine	Oscillatoriales	Florida
Capilliphycus	Caires et al. 2019	Marine	Oscillatoriales	Brazil
Cephalothrix	Malone et al. 2015	Lake	Oscillatoriales	Brazil
Crocosphaera	Mareš et al. 2019	Marine	Chroococcales	Brazil
Cryptococcum	Gama et al. 2019	Terrestrial	Chroococcales	Brazil
Dapis	Engene et al. 2018	Marine	Oscillatoriales	Florida
Dapisostemon	Hentschke et al. 2016	Epidendric	Nostocales	Brazil
Desikacharya	Saraf et al. 2019a	Freshwater	Nostocales	India
Dictyophoron	Komárek et al. 2017	Bentic	Nostocales	Belize
Dulcicalothrix	Saraf et al. 2019b	Oligotrophic lake	Nostocales	India
Elainella	Jahodářová et al. 2018	Planktic	Synechococcales	Vietnam
Euryhalinema	Chakraborty et al. 2019	Soil	Synechococcales	India
Ewamiania	McGregor & Sendall 2017a	Thermal springs	Nostocales	Australia
Foliisarcina	Alvarenga et al. 2016	Aerophytic	Pleurocapsales	Brazil
Goleter	Miscoe et al. 2016	Cave wall	Nostocales	Hawaii
Gloeomargarita	Moreira et al.2017	Lake biofilm	Gloeomargaritales	Mexico
Halotia	Genuário et al. 2015	Mangrove soil	Nostocales	Brazil
Chamaethrix	Dvořák et al. 2017	Soil crust	Synechococcales	Florida
Chroakolemma	Becerra–Absolón et al. 2018	Desert soil	Synechococcales	Mexico
Inacoccus	Gama et al. 2019	Terrestrial	Chroococcales	Brazil
Iningainema	Mc.Gregor & Sendall 2017b	Spring	Nostocales	Australia
Jacksonvillea	Hašler et al. 2017	Bentic	Oscillatoriales	Florida
Komarekiella	Hentschke et al. 2017	Aerophytic	Nostocales	Brazil
Komarkovaea	Mai et al. 2018	Waterfalls	Synechococcales	Puerto Rico
Kovacikia	Miscoe & Johansen 2016	Cave wall	Synechococcales	Hawaii
Kryptousia	Alvarenda et al. 2017	Aerophytic	Nostocales	Brazil
Lagosinema	Akagha et al. 2019	Brackish	Synechococcales	Nigeria
Leptoelongatus	Chakroborty et al. 2019	Soil	Synechococcales	India
Macrochaete	Berrendero et al. 2016	Soil crust	Nostocales	Brazil, Spain
Marileptolyngbya	Zhou et al. 2018	Marine	Synechococcales	China
Minunostoc	Cai et al. 2019	Epilithic	Nostocales	China
Myxacorys	Pietrasiak et al. 2019	Soil crust	Synechococcales	Chile
Neolyngbya	Caires et al. 2017/18	Bentic marine	Oscillatoriales	Brazil
Neowollea	Tawong et al. 2019	Freshwater	Nostocales	Thailand
Nunduva	González–Resendiz et al. 2018	Marine	Nostocales	Mexico
Onodrimia	Jahodářová et al. 2017	Epixylon	Synechococcales	Java, Indonesia
Pantanalinema	Vieira Vaz et al. 2015	Saline wetland	Synechococcales	Brazil
Pelatocladus	Miscoe et al. 2016	Cave wall	Nostocales	Hawaii
Perforafilum	Zimba et al. 2020	Hypersaline	Oscillatoriales	Texas

Table 1 Cont.

Phyllonema	Alvarenga et al. 2016	Aerophytic	Nostocales	Brazil, Mexico
Potamolinea	Martins & Branco 2016	Stream	Oscillatoriales	Brazil
Potamosiphon	McGregor & Sendall 2019	Epilithic	Oscillatoriales	NE Australia
Purpureonostoc	Cai et al. 2020a	Soil	Nostocales	Tibet, China
Pycnacronema	Martins et al. 2018	Aerophytic	Oscillatoriales	Brazil
Reptodigitus	Casamatta et al. 2020	Epizoic	Nostocales	Florida
Rippkaea	Mareš et al. 2019	Terrestrial	Chroococcales	Taiwan
Salileptolyngbya	Zhou et al. 2018	Marine	Synechococcales	China
Sinocapsa	Wang et al. 2019	Aerophytic	*Ordo incertae sedis*	China
Sodaleptolyngbya	Cellamare et al. 2018	Stromatolites	Synechococcales	Mayotte Island
Sodalinema	Cellamare et al. 2018	Planktic	Synechococcales	Mayotte island
Stenomitos	Miscoe et al. 2016	Cave wall	Synechococcales	Hawaii
Toxifilum	Zimba et al. 2017	Bentic	Synechococcales	Texas
Violetonostoc	Cai et al. 2020b	Epilithic	Nostocales	China
Zehria	Mareš et al. 2019	Marine	Chroococcales	Florida

et al. 1993, 1997; Gold–Morgan et al. 1994; Komárek & Komárková–Legnerová 2002, 2007; Sant´Anna et al. 2010; Fiore et al. 2007).

Compared to temperate regions, the tropics span a larger continuous geographic area. Coupled with relatively low seasonality and high humidity, this may enable many species to coexistence (Mittelbach et al. 2007). For example, subaerial microalgae have higher diversity in tropical/subtropical, subaerial habitats compared to temperate ecosystems (Eldridge 2001; Ortega–Morales et al. 2006; Neustupa & Škaloud 2008; Keshari & Adhikary 2014; Sherwood et al. 2015; Nguyen et al. 2017). Moreover, cyanobacteria were found to be the second most abundant group of algae in these habitats, particularly in open spaces with higher light intensities (Neustupa & Škaloud 2008). Cyanobacteria possess several advantages (e.g., sheath production, accessory pigments, baeocytes, etc.) that may allow them to thrive in these high light habitats (Villanueva et al. 2019a,b).

Cyanobacterial adaptability

Cyanobacteria are unique by the wide range of adaptations to environmental conditions. Tropical zones include habitats from deserts to rainforests covering gradients of temperature, light, water and nutrient availability. Sheath/mucilage production in cyanobacteria represent an adaptation to water content fluctuation and is especially important in developing the structure of soil biological crusts (Belnap et al. 2001; Pietrasiak et al. 2019). Sheaths contain UV protective molecules like scytonemin or gloeocapsin (Fleming & Castenholz 2007), and this mucilage is responsible for the gliding motility of cyanobacteria (Hoitzyk 2000). Cyanobacteria excel at elevated temperatures (Sinetova et al. 2017; Pedersen & Miller 2017). N–fixation capacities of cyanobacteria comprise an advantage in nutrient limited tropical environments (Charpy et al. 2010; Mareš et al. 2019). Lastly, the unrivalled capacity for extensive chromatic adaptation allows tolerance of both low and high light conditions. Phycobilins allow photon capture between the blue and red regions of the spectrum that are not efficiently trapped by chlorophyll (Kehoe 2010). If the environment proves too inhospitable, cyanobacteria can also produce resting cells (akinetes).

Endemic vs. cosmopolitan taxa

There is currently much debate pertaining to the notion of endemic vs. cosmopolitan microbes in general (e.g., Finlay 2002; Dvořák et al. 2012). Echoing this debate, cyanobacterial researchers are increasingly willing to erect new genera based on putatively endemic organisms (e.g., Flechtner et al. 2002; Casamatta et al. 2006). For example, the genus *Brasilonema,* originally described from Brazil (Fiore et al. 2007), has been found to have wider distribution (Becerra–Absalon et al. 2013; Vaccarino & Johansen 2012; Villanueva et al. 2019a; Barbosa et al. 2021). Moreover, studies show that the distribution pattern may rather be taxa specific and any general pattern cannot be drawn among the cyanobacteria.

Conversely, the ubiquitous cyanobacteria *Synechococcus* and *Prochlorococcus* have traditionally been considered global and cosmopolitan in marine habitats, yet recent evidence has challenged this notion. Molecular evidence points to several distinct genetic lineages of both genera, indicating more habitat preferences than previously assumed (Zwirglmaier et al. 2007, 2008; Ahlgren & Rocap 2012; Mazard et al. 2012). Dvořák et al. (2012) point out that the cosmopolitan mat–forming

Microcoleus vaginatus exhibits episodic genetic isolation which mimics a perceived biogeographic pattern.

Even when a taxon evolves in a tropical habitat, it may expand its range as the environment changes. For example, the common planktonic cyanobacterium, *Raphidiopsis raciborskii*, was initially considered a strict tropical taxon. Yet as climate changes and temperatures increase, it has been considered to be a microbial invader throughout North America (Gugger et al. 2005; Kling 2009) and the temperate zone (Aguilera et al. 2018). This increased geographical range may be the result of environment changes (Briand et al. 2004; Dvořák & Hašler 2007; Bonila et al. 2016), a result of allelopathic potential (Branco & Senna 1994; Antunes et al. 2015), or innate ecophysiological tolerances (Padisák 1997; Antunes et al. 2015). The great degree of genetic divergence within this lineage (Moreira et al. 2011; Wood et al. 2014) also revealed that radiation within continents is more probable than the recent exchange between continents (Haande et al. 2008; Ribeiro et al. 2020). Thus still, it is not certain whether the expansion of *Raphidiopsis raciborskii* from tropical habitats is a result of enormous ecophysiological range or existence of ecologically differentiated ecotypes (Antunes et al. 2015). Likewise, the putatively tropical genus *Komarekiella* was described from Brazil and Hawaii (Hentschke et al. 2017), but was morphologically indistinguishable to *Chlorogloeopsis*, with vast cultural phenotypic plasticity. However, this genus has subsequently been recovered from additional habitats in Florida, so the distribution may be more limited by researcher's ability to culture and identify it, rather than eco–physiological constraints (Brown et al. 2021).

Patterns of distribution may be difficult to articulate, as evidenced by the common, cosmopolitan, taxon *Microcystis aeruginosa*. Van Gremberghe et al. (2011) and Ribeiro et al. (2020) did not find any morphological or genetic diversity in *Microcystis aeruginosa* using single gene analyses. However, studies based on a concatenated set of four loci revealed some genetic diversity in this species (Moreira et al. 2014). They proposed an early origin of *M. aeruginosa* in the African continent, with subsequent European populations having a cosmopolitan distribution. However, Capelli et al. (2017) found significant genetic differences (including differences in capability to synthesize microcystins) among another global, cosmopolitan taxon, *Dolichospermum lemmermannii,* isolates.

Some level of endemism maybe expected in "island environments", such as hot geothermal springs (Papke et al. 2003, Whitaker et al. 2003). Indeed, the occurrence of both endemic and cosmopolitan species (with respect to temperature) from other thermal environments has been witnessed in Zerka Ma´in hot springs (Ionescu et al. 2010). The "island effect" may also be common in other unusual habitats, such as hypogean, subterranean, and cave systems. For example, while *Albertania skiophila* has been described as endemic to Maltese hypogea (Zammit 2018), the biodiversity of these environments is poorly known, and thus additional research of caves and catacombs is necessary (Lampriou et al. 2013; Miscoe et al. 2016).

Undersampling of tropical cyanobacteria

One possible reason for the lack of perceived tropical diversity could be attributed to sampling efforts (sensu Finlay 2002). The vast majority of described cyanobacterial taxa have been from temperate regions; not coincidentally, this is where the majority of cyanobacterial researchers reside. To illustrate this bias, we present a map of a number of identified cyanobacteria in the tropical countries (Fig. 1). We found that only Cuba, Mexico, Brazil and Argentina have high number of identified species in South and Central America. As a whole, the African continent seems to be less studied. Most of the countries have unknown diversity, with the most studied being Ethiopia, Ghana, Republic of the Congo, and Sierra Leone. The best studied regions in Asia were India, Nepal, Myanmar, Bangladesh, China, and Vietnam. Australia has well–studied cyanobacterial diversity as well, likely due to the presence of researchers and concerns about eutrophication.

However, recent works by researchers from tropical habitats have begun to greatly expand our knowledge of diversity (see references elsewhere). In a review of Web of Science papers from February 22, 2021, we note that 5771 papers pertain to the "diversity of cyanobacteria", while a mere 394 deal with "tropical diversity of cyanobacteria", most of which are limited floristic studies based solely on morphological examination of samples (see problems with cryptic diversity above). There were no such papers indexed at Web of Science dealing with a tropical diversity of cyanobacteria until 1994. Since 1995, however, interest has rapidly increased, nearing 40 papers per year in 2020 (Fig. 2).

Another potential reason for the dearth in tropical sampling is that not all cyanobacteria are equally "important" to human endeavors. For example, *Microcystis aeruginosa* is very commonly encountered as a toxic taxon and thus is often sequenced. Further, planktonic taxa are commonly sequenced due to their prevalence, ubiquity, and visibility to researchers (Poulíčková et al. 2014). Conversely, many other cyanobacterial taxa may not be sequenced enough (for example, those from unusual habitats or those not typically considered "nuisance" taxa). In the end, it may be that questions pertaining to tropical diversity are intimately related to the phylogenetic markers employed (see above). Thus, it appears that the question of tropical cyanobacterial endemism and biogeographical patterns in general depends on the level of resolution and markers employed.

Driving factors of microbial diversity

Latitudinal gradients are considered primary factors in the distribution and diversity of plants and animals (for a review see Mittelbach et al. 2007). Species diversity increases as one travels closer to the equator (Hillebrandt 2004), although some lineages exhibit inverse latitudinal gradients (Kindlmann et al. 2007). Using fossil records, Mannion et al. (2014) noted that peaks in tropical species diversity seem to be restricted to intervals of the Palaeozoic and the past 30 million years. Bromham & Cardillo (2003) suggest that rates of mutagenesis and evolutionary divergence increase closer to the equator; although this work was from macroscopic eukaryotes, and the application to microbes remains unknown. Conversely, Passy (2010) has reported an exception to this general pattern in her study of continental lotic water diatoms from the U.S., which exhibit a U–shaped latitudinal distribution of richness. Wright et al. (2006) calculated a doubling rate of nucleotide substitutions in the tropics, but no one has calculated such a rate using cyanobacteria. Evolutionary scenarios might explain this phenomenon. First, diverse resources may support more specialized organisms, which in turn may foster greater amounts of productivity (Bromham & Cardillo 2003). Second, biological processes (e.g. reproduction, speciation) are faster in elevated temperatures because of faster kinetics of biological processes (Evans et al. 2005; Gillooly et al. 2005).

The factors that influence bacterial latitudinal diversity are subject to intensive debate in the literature. For example, in a review and meta–analysis of 111 studies by Lozupone & Knight (2007), they conclude that it is salinity, and not extremes of temperature, pH, or other physical and chemical parameters, that is the most important parameter structuring bacterial communities. Conversely, in a review by Horner–Devine et al. (2004), the authors note that bacterial biodiversity follows the same patterns observed in plants and animals. When examining marine bacterioplankton, Fuhrman et al. (2008) showed that latitudinal patterns are similar in plants and animals, with temperature being a driving factor. Marine bacterioplankton exhibit significantly increased numbers of detected genotypes towards the equator. A meta–analysis of 3502 sampling experiments performed by Tamames et al. (2010) revealed salinity, temperature, and animal tissue type as the most important selective environmental characteristics. Soininen (2012) echoed this latitudinal pattern in a review of macroecology of unicellular organisms. Stomp et al. (2011) posited that strong latitudinal, longitudinal and altitudinal gradients all impact the diversity and distribution of phytoplankton from 540 lakes across North America. Thus, it appears that the factors most important for distribution and biodiversity of microbes in general, and cyanobacteria in particular, appear to be difficult to untangle and perhaps subject to myriad forces not always evident to researchers.

Trends and perspectives

Several potential future endeavors will greatly expand our knowledge of tropical cyanobacterial diversity. First, more extensive, comprehensive floristic surveys in these habitats need undertaking. Identification keys from tropical regions should be expanded and updated. Further, attention to seldom sampled geographic regions, countries, and habitats (e.g., subaerial, benthic, endolithic) needs to be increased (Neustupa & Škaloud 2008; Poulíčková et al. 2014). Second, more attention to molecular markers for taxonomic identification is of great importance. This will help ameliorate issues arising from cryptic diversity. However, it must be noted that sequences from GenBank may be misidentified or inaccurate, so a better method of validating sequences and taxonomic assignments will be warranted. Third, hypotheses relating to elevated rates of evolution (i.e., via increased substitution rates) can be explored and tested by researchers. Fourth, biogeographic patterns can be elucidated by more nuanced approaches (e.g., genomic analyses, molecular markers), rather than relying merely upon morphological examinations.

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Author contributions
P. Dvořák: original concept, drafting; P. Hašler: taxonomy, editing; A. Poulíčková: literature search, manuscript editing, formatting; D. Casamatta: drafting, editing, English and style unification

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