Received: 31 October 2019 | Revised: 8 July 2020 | Accepted: 20 July 2020

DOI: 10.1111/geb.13173

RESEARCH PAPER

Global Ecology and Biogeography A Journal of Macroecology WILEY

Contrasting environmental preferences of photosynthetic and non-photosynthetic soil cyanobacteria across the globe

Concha Cano-Díaz[1] | Fernando T. Maestre[2,3] | David J. Eldridge[4] | Brajesh K. Singh[5,6] | Richard D. Bardgett[7] | Noah Fierer[8,9] | Manuel Delgado-Baquerizo[10]

[1]Departamento de Biología, Geología, Física y Química Inorgánica, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, Móstoles, 28933, Spain

[2]Instituto Multidisciplinar para el Estudio del Medio "Ramón Margalef", Universidad de Alicante, Edificio Nuevos Institutos, Carretera de San Vicente del Raspeig s/n, San Vicente del Raspeig, 03690, Spain

[3]Departamento de Ecología, Universidad de Alicante, Carretera de San Vicente del Raspeig s/n, San Vicente del Raspeig, 03690, Spain

[4]Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales, Australia

[5]Global Centre for Land-Based Innovation, University of Western Sydney, Penrith, New South Wales, Australia

[6]Hawkesbury Institute for the Environment, University of Western Sydney, Penrith, New South Wales, Australia

[7]Department of Earth and Environmental Sciences, The University of Manchester, Manchester, UK

[8]Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO, USA

[9]Cooperative Institute for Research in Environmental Sciences, University of Colorado, Boulder, Colorado, USA

[10]Departamento de Sistemas Físicos, Químicos y Naturales, Universidad Pablo de Olavide, Sevilla, 41013, Spain

Correspondence
Concha Cano-Díaz, Departamento de Biología, Geología, Física y Química Inorgánica, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, Campus de Móstoles, Calle Tulipán s/n, 28933 Móstoles, Madrid, Spain.
Email: conchacanodiaz@gmail.com

Funding information
H2020 European Research Council, Grant/Award Number: 242658 [BIOCOM] and 647038 [BIODESERT]; Department for Environment, Food and Rural Affairs, Grant/Award Number: BD5003; Spanish Ministry of Economy and Competitiveness, Grant/Award Number: BIOMOD project, ref. CGL2013-44661-R; Spanish Ministry of Science and Innovation, Grant/Award Number: (RYC2018-025483-I); British Ecological Society No LRB17\1019 [MUSGONET]; Australian Research Council, Grant/Award Number: DP170104634; Biotechnology and Biological Sciences Research Council, Grant/Award Number: BB/L026406/1; Generalitat Valenciana, Grant/Award Number: BIOMORES project, ref. CIDEGENT/2018/041

Editor: Stephanie Kivlin

Abstract

Aim: Cyanobacteria have shaped the history of life on Earth and continue to play important roles as carbon and nitrogen fixers in terrestrial ecosystems. However, their global distribution and ecological preferences remain poorly understood, particularly for two recently discovered non-photosynthetic cyanobacterial classes (Sericytochromatia and Melainabacteria).

Location: Two hundred and thirty-seven locations across six continents encompassing multiple climates (arid, temperate, tropical, continental and polar) and vegetation types (forests, grasslands and shrublands).

Time period: Sampling was carried out between 2003 and 2015.

Major taxa studied: Photosynthetic and non-photosynthetic cyanobacterial taxa.

Methods: We conducted a field survey and used co-occurrence network analysis and structural equation modelling to evaluate the distribution and environmental preferences of soil cyanobacteria across the globe. These ecological preferences were used to create a global atlas (predictive distribution maps) of soil cyanobacteria.

Results: Network analyses identified three major groups of cyanobacterial taxa, which resembled the three main cyanobacterial classes: the photosynthetic Oxyphotobacteria-dominated cluster, which were prevalent in arid and semi-arid areas, and the non-photosynthetic Sericytochromatia- and Melainabacteria-dominated

clusters, which preferred hyper-arid oligotrophic and acidic/humid environments, respectively.

Main conclusions: This study provides new insights into the environmental preferences of non-photosynthetic cyanobacteria in soils globally. Our findings highlight the contrasting environmental preferences among the three clusters of cyanobacteria and suggest that alterations in environmental conditions linked to climate change might result in important changes in the ecology and biogeography of these functionally important microorganisms.

KEYWORDS

16S amplicon sequencing, cyanobacteria, global distribution, microbial biogeography, microbial network, non-photosynthetic cyanobacteria

1 | INTRODUCTION

Cyanobacteria are microorganisms responsible for some of the most important events in Earth's history, including the rise of oxygen levels via oxygenic photosynthesis (Dismukes et al., 2001; Rasmussen, Fletcher, Brocks, & Kilburn, 2008) and the formation of plastids through endosymbiosis (Margulis, 1970; Mereschkowsky, 1905;). Despite being one of the most studied microbial groups (Castenholz et al., 2001; Garcia-Pichel, Belnap, Neuer, & Schanz, 2003; Garcia-Pichel, 2009; Whitton & Potts, 2012), there are still major knowledge gaps associated with the diversity and global distribution of these organisms. Recent studies have revealed the existence of two new bacterial clades closely related to cyanobacteria, 4C0d-2 (Melainabacteria) and ML635J-21 (Sericytochromatia), recently proposed as new classes of phylum Cyanobacteria (Soo, Hemp, Parks, Fischer, & Hugenholtz, 2014; Soo et al., 2017). These non-photosynthetic classes are included in the latest releases of the most commonly used rRNA databases, Silva and Greengenes (DeSantis et al., 2006; Quast et al., 2013). Unlike photosynthetic cyanobacteria (hereafter, class Oxyphotobacteria), these clades have no genes associated with photosynthesis and have provided a new perspective on the phylum, broadening our understanding of the functional capabilities of cyanobacteria and their evolutionary origin.

The construction of metagenome-assembled genomes has enabled the assessment of the metabolic potential of these organisms, suggesting that Melainabacteria and Sericytochromatia are chemoheterotrophs with metabolisms mostly centred on fermentation (Di Rienzi et al., 2013; Soo et al., 2014, 2017; Soo, 2015). Additionally, no genes for phototrophy or carbon (C) fixation have been found in Melainabacteria and Sericytochromatia (Soo et al., 2017), indicating that oxygenic photosynthesis could be a trait acquired later in Oxyphotobacteria by horizontal gene transfer (Raymond, Zhaxybayeva, Gogarten, Gerdes, & Blankenship, 2002). Such physiological and genetic differences might result in contrasting ecological preferences for these novel cyanobacterial taxa, but empirical evidence for this is lacking.

Soil-borne Oxyphotobacteria are widely distributed on Earth (Garcia-Pichel et al., 2003; Moreira, Vasconcelos, & Antunes, 2013; Whitton & Potts, 2012) but they are particularly predominant in hot, arid and polar regions with sparse plant cover. They are an important component of biocrusts, soil surface communities dominated by lichens, mosses, cyanobacteria and associated microorganisms (Belnap et al., 2016) and play key ecological roles in these environments by regulating crucial soil processes, such as nitrogen (N) and C fixation, soil stabilization and infiltration/runoff (Mager & Thomas, 2011; Sciuto & Moro, 2015). Other terrestrial cyanobacterial communities grow on the surface or inside rocks and soil (endolithic and subsoil forms) and are well adapted to dry conditions and high- or low-irradiation regimens (Domínguez & Asencio, 2011; Puente-Sánchez et al., 2018; Warren-Rhodes et al., 2006). The capacity of Oxyphotobacteria to remain dormant for long periods of time is also a fundamental characteristic of these organisms, which allows them to survive in extreme environments characterized by high or low temperatures, desiccation regimens or high ultraviolet (UV) radiation (Garcia-Pichel, 2009; Quesada & Vincent, 2012; Whitton & Potts, 2012).

Local and regional studies show that soil Oxyphotobacteria are generally considered to prefer neutral to alkaline pH for optimal growth (Brock, 1973; Nayak & Prasanna, 2007; Whitton & Sinclair, 1975). However, the global biogeography of soil Oxyphotobacteria has not been fully resolved owing to the concentration of cyanobacterial research in particular regions, for example, studies in the western USA or the Antarctic continent (Büdel, Dulić, Darienko, Rybalka, & Friedl, 2016; Garcia-Pichel, López-Cortés, & Nübel, 2001; Garcia-Pichel et al., 2003; Moreira et al., 2013; Namsaraev, Mano, Fernandez, & Wilmotte, 2010; Williams, Loewen-Schneider, Maier, & Büdel, 2016) and the focus given to key and abundant taxa, such as *Microcoleus vaginatus* or the genus *Chroococcidiopsis* (Bahl et al., 2011; Dvořák, Hašler, & Poulíčková, 2012), or specific habitats, such as cold ecosystems and deserts (Bahl et al. 2011; Jungblut et al., 2010). There are clear gaps concerning their distribution in certain regions of the world, such as South America (Büdel et al., 2016). Despite their wide dispersal ability, attributable to their small

size, aeolian transport and tolerance to desiccation and irradiation (Billi, Friedmann, Hofer, & Caiola, 2000; Kellogg & Griffin, 2006), and their often cosmopolitan distribution (Flombaum et al., 2013; Garcia-Pichel, Prufert-Bebout, & Muyze, 1996; Taton et al., 2006), current knowledge suggests a more complex biogeography of these microorganisms that is likely also to be influenced by their phylogeny and historical legacies (Flombaum et al., 2013; Garcia-Pichel et al., 1996, 2003; Nayak & Prasanna, 2007; Taton et al., 2006).

The ecology and biogeography of the non-photosynthetic cyanobacterial classes (Melainabacteria and Sericytochromatia) in soils is poorly known. Available information on these organisms comes from genomes from aphotic environments, such as animal guts or subsurface groundwater, and artificial systems, such as water treatment facilities and laboratory bioreactors (Di Rienzi et al., 2013; Ley et al., 2005; Soo et al., 2014; Utami et al., 2018; Warnecke et al., 2007; Yagi, Neuhauser, Ripp, Mauro, & Madsen, 2010), and the scarce environmental studies correspond only to aquatic ecosystems, such as lakes and algal biofilms (Monchamp et al., 2018; Monchamp, Spaak, & Pomati, 2019).

To advance our understanding of the biogeography and ecological preferences of soil photosynthetic and non-photosynthetic cyanobacteria, we used data from a global soil survey covering a wide diversity of climate, soil and vegetation types (Delgado-Baquerizo et al., 2018). We expected the distinct ecological attributes of photosynthetic and non-photosynthetic cyanobacteria to be associated with very different environmental preferences. For example, we know that some Oxyphotobacteria have developed highly competitive adaptations to thrive in arid soils with low soil organic C and plant productivity (Lund, 1967; Maestre et al., 2015; Whitton & Sinclair, 1975). In these environments, we expect Oxyphotobacteria to dominate owing to their capacity to build protective sheath pigments and to fix atmospheric C and N, which can be an important ecological advantage. However, Oxyphotobacteria are also expected to appear in a wide variety of environmental conditions, including low-light, low-oxygen or even anoxygenic environments, owing to their enormous functional diversity (Adams & Duggan, 1999; Garcia-Pichel, 2009; Puente-Sánchez et al., 2018; Stal & Moezelaar, 1997). Conversely, non-photosynthetic cyanobacteria rely on soil organic C pools to grow, which could translate into contrasting preferences related to soil nutrient availability. We expect to find groups of taxa co-occurring and sharing similar environmental preferences (hereafter, ecological clusters) related to photosynthetic capability, habitat preferences and historical legacies.

2 | MATERIALS AND METHODS

2.1 | Global survey: Sites, soil collection, and soil and molecular analyses

We used 16S rRNA gene amplicon sequencing data from a global survey of 237 locations (Supporting Information Figure S1) across six continents encompassing multiple climates (arid, temperate, tropical, continental and polar) and vegetation types (forests, grasslands and shrublands) (Delgado-Baquerizo et al., 2018). A composite soil sample (0–7.5 cm depth) was collected under the dominant vegetation at each surveyed location. A fraction of each sample was immediately frozen at −20°C for molecular analyses; the other fraction was air dried for chemical analyses. Sample collection of soils took place between 2003 and 2015. We do not expect differences in the timing of sample collection to have a large effect on our results for two reasons. First, at the global scale seasonal variability is expected to be dominated by cross-biome variability (e.g., see Carini et al., 2020 on the importance of spatial versus temporal scales when analysing soil microbial communities). To put this simply, a dryland and a boreal forest are so different that they would typically harbour distinct microbial communities regardless of their seasonal variability. Second, we are using amplicon sequencing DNA-based analyses (as described at the end of this section), which characterize not only the active portion of cyanobacterial communities but also the dormant one at the time of sampling (Li et al., 2017). The soils sampled comprise a wide variety of physicochemical properties; pH ranged from 4.04 to 9.21, texture of the fine fraction (percentage of clay and silt) from 1.4 to 92.0%, soil total organic carbon (OC) from 0.15 to 34.77%, soil total nitrogen (TN) from 0.02 to 1.57, C:N ratio (CN) from 2.12 to 67.52 and soil total phosphorus (TP) from 75.10 to 4111.04 mg P/kg soil. These analyses were performed using standard laboratory methods described by Delgado-Baquerizo et al. (2018).

Climatic variables [maximum and minimum temperature (MAXT and MINT), precipitation seasonality (inter-annual coefficient of variation in precipitation, PSEA) and mean diurnal temperature range (MDR)] were obtained for each site from the WorldClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). The aridity index (precipitation/potential evapotranspiration) was obtained from the Global Potential Evapotranspiration database (Zomer, Trabucco, & Bossio, 2008), which uses interpolations from WorldClim. The annual UV index, a measure of the risk of UV exposure ranging from zero (minimal risk) to 16 (extreme risk), was obtained for each site using data from the Aura satellite (Newman & McKenzie, 2011). Net aboveground primary productivity (ANPP) was estimated with satellite imagery using the normalized difference vegetation index (NDVI) from the Moderate Resolution Imaging Spectroradiometer (MODIS) aboard NASA's Terra satellites (Justice, Vermote, Defries, & Roy, 1998). This index provides a global measure of the greenness of the Earth for a given period (Pettorelli et al., 2005). Here, we used monthly averaged values for NDVI for the sampling period between 2003 and 2015 (10 km resolution).

Microbial DNA was extracted using the PowerSoil DNA Isolation Kit (MoBio Laboratories, Carlsbad, CA, USA) following the manufacturer's instructions. DNA extracts were sequenced by targeting the bacterial V3–V4 region using 16S rRNA gene primers 341F (CCTACGGGNGGCWGCAG) and 805R (GACTACHVGGGTATCTAATCC) and the Illumina Miseq platform

of the Next Generation Genome Sequencing Facility at Western Sydney University (NSW, Australia).

Bioinformatic analyses were performed with a combination of QIIME (Caporaso et al., 2010), USEARCH (Edgar, 2010) and UPARSE (Edgar, 2013). After merging the reads, the primers were trimmed and sequences of low quality (expected error rate greater than one) discarded. Phylotypes were defined with UCLUST (Edgar, 2010) at an identity level of 97%, and taxonomy was assigned using Silva Incremental Alligner *Search and classify* (www.arb-silva.de/act) with the Silva database (complementing not identified phylotypes with Greengenes database) (DeSantis et al., 2006; Quast et al., 2013). Phylotypes represented by only a single read (singletons) were removed. The final dataset of phylotypes was filtered for phylum Cyanobacteria (excluding chloroplast), and the relative abundance of each cyanobacterial phylotype in relationship to total bacteria (all 16S rRNA reads) was calculated.

2.2 | Structure of the community: Network analyses

To explore the different patterns of cyanobacterial co-occurrence across our samples, we conducted a network analysis with the CoNet software (Faust & Raes, 2016). This tool detects significant non-random patterns of co-occurrence using multiple correlation and dissimilarity measures. Two correlation coefficients (Pearson's and Spearman's) and dissimilarity distances (Bray–Curtis and Kullback–Leibler) were used to obtain a more reliable network (Faust & Raes, 2012). When links were detected by more than one correlation/dissimilarity measure, they were considered as a single link. Samples were standardized before network analyses with the "col_norm" function, which divides each column by its sum, converting abundances in column-wise proportions. We computed the network with the top 1,000 links for each measure and tested the statistical significance of each link with 1,000 permutations and the function "shuffle rows" as the resampling strategy. We tested for multiple comparisons using the Benjamini–Hochberg procedure (Benjamini & Hochberg, 1995), keeping links with an adjusted merged p-value $< .05$. The final network was visualized with the interactive platform gephi (Bastian, Heymann, & Jacomy, 2009). We obtained the ecological clusters with the function "fastgreedy" from the igraph package (Csárdi & Nepusz, 2006) in R v.3.4.0 (R Core Team, 2013) and tested the statistical significance of modularity using 10,000 random networks. Network analysis allowed us to divide the community between ecological clusters, which we used for downstream analysis. The relative abundance of each ecological cluster per sample was calculated by averaging the standardized (z-score) relative abundance of the phylotypes present within each ecological cluster. Thus, we obtained a balanced contribution of each cyanobacterial phylotype to the relative abundance of its ecological cluster. Note that the use of z-score standardization transforms relative abundances and, therefore, negative values can be obtained.

2.3 | Factors determining cyanobacterial global distribution

2.3.1 | Environmental effects

We conducted structural equation modelling (Grace, 2006) to evaluate the direct and indirect effects of spatial, climatic, vegetation and soil variables as predictors of the abundance of the main cyanobacterial ecological clusters (for our a priori model, see Supporting Information Figure S2). This approach is useful for simultaneously testing the influence of multiple variables and the separation of direct and indirect effects of the predictors included in the model (Grace, 2006). These included spatial (latitude, sine longitude and cosine longitude), climatic [MDR, MAXT, MINT, PSEA and Aridity (1 − aridity index)] and vegetation (grassland, forest and ANPP) variables, in addition to soil properties (CN, soil OC, pH and the percentage of clay and silt). Before modelling, we transformed them to improve normality: Aridity, OC, PSEA and CN were $\log_{10}$-transformed, and both ANPP and the percentages of clay and silt were square root transformed. We used the Chi-squared Goodness of Fit test, supplemented with the root mean square error of approximation (RMSEA), to test the overall fit of the model. We analysed path coefficients of the model and their associated p-values and the total effects of each variable. Given that some of the variables were not normally distributed despite transformation, we used 5,000 bootstraps to test the significance of each path simultaneously. Structural equation modelling analyses were conducted using AMOS v.24.0.0 (IBM SPSS, Chicago, IL, USA).

To obtain a prediction of the potential distribution of the main cyanobacterial ecological clusters, we used the regression model Cubist (Quinlan, 2014) as implemented in the R package Cubist (Kuhn, Weston, Keefer, Coulter, & Quinlan, 2016). This model uses a linear regression tree analysis that predicts the most important factors affecting the abundance of each ecological cluster based on environmental covariates. Covariates in our models included the same variables used in our structural equation models. Global predictions of the distribution of major clusters were done on a 25 km × 25 km resolution grid. Soil properties for this grid were obtained from SoilGrids (Hengl et al., 2017). Major vegetation types (grasslands and forests) were obtained using the Globcover2009 map from the European Space Agency (Bontemps et al., 2013). Information on climate, UV index and net primary productivity were obtained from the WorldClim database and NASA satellites as described above.

We conducted multiple analyses to support the validity of our global prediction maps. First, we used kernel density estimations to compare the distribution of key soil and climate variables of our dataset with those from high-resolution global maps: SoilGrids (Hengl et al., 2017) and WorldClim (Hijmans et al., 2005). Our dataset comprises a large percentage of their global variability (Supporting Information Figure S3): 78.51% for OC, 94% for pH, 58.25% for aridity, 45.98% for PSEA, 71.63% for MINT, 47.03%

for MAXT and 96.43% for ANPP. These results indicate that our sampling covers a large proportion of the environmental variability found on Earth. Second, we found a strong correlation between the relative abundance of our cyanobacterial ecological clusters and key microbial environmental factors at the global scale (see Results below), which suggests that environmental data can be used to predict their distribution. Finally, predictive maps were cross-validated with an independent dataset obtained from the Earth Microbiome Project (EMP; Thompson et al., 2017), which contains data on soil cyanobacteria from 403 sites worldwide (see Supporting Information Figure S1). For this, we estimated the relative abundance of the three main cyanobacterial clusters for the EMP dataset using the 97% similar EMP phylotypes. We first calculated relative abundance of each cyanobacterial phylotype in relationship to total bacteria (all 16S rRNA reads of the EMP dataset). Then, the relative abundance of each ecological cluster per sample was computed by averaging the standardized (*z*-score) relative abundance of the phylotypes of each ecological cluster, as explained above for our dataset. We then used our predictive maps to extract the predicted relative abundance of each cluster for the EMP locations. These predictive abundances were then compared with the independent results of the relative abundance of each cluster calculated with the EMP dataset using Pearson correlations.

We also conducted a permutational multivariate analysis of variance (PERMANOVA) with Bray–Curtis distance measure to evaluate the effect of vegetation type on the abundance of each cyanobacterial cluster with the *adonis* function and 1,000 permutations. To test for the differences in the relative abundance of each cluster across vegetation types, we first tested the homogeneity of groups dispersions (variances) with *betadisper* function, and from the result we performed the post hoc analysis Tukey's honestly significant difference with the *TukeyHSD* function. All these analysis were performed with vegan v.2.4-2 (Oksanen, 2015) and R v.3.6.0 (R Core Team, 2013).

2.3.2 | Phylogenetic tree

The phylogenetic tree of cyanobacteria was constructed using the SILVA Alignment, Classification and Tree (ACT) Service (www.arb-silva.de/act). Multiple sequence alignment of the 343 rRNA gene sequences was performed using SINA v.1.2.11 (Pruesse, Peplies, & Glöckner, 2012). The phylogenetic tree was obtained with their built-in tree computation tool FastTree (Price, Dehal, & Arkin, 2009) using the general time reversible (GTR) model of nucleotide evolution (Nei & Kumar, 2000) and keeping the default parameters. The display and annotation of the phylogenetic tree were made with iTol v.5.5 (Letunic & Bork, 2019).

3 | RESULTS

3.1 | Global cyanobacterial co-occurrence patterns

Despite the common and widespread occurrence of soil cyanobacterial taxa on Earth, no single sample contained all 343 phylotypes. The most ubiquitous cyanobacterial phylotype, *Microcoleus vaginatus*, was detected in 113 of the 237 sites surveyed. Moreover, the relative abundance of cyanobacterial phylotypes in our soils ranged from 0.01 to 4.35% of all bacterial 16S rRNA gene sequences (see Supporting Information Table S1). The cyanobacterial orders with the highest relative abundances included Oscillatoriales (Oxyphotobacteria), followed by Obscuribacterales (Melainabacteria) and Nostocales (Oxyphotobacteria) (Figure 1). Non-photosynthetic phylotypes appeared in almost all samples (235 of 237 samples; 99.2%). Photosynthetic cyanobacteria phylotypes appeared in the majority of samples (185 of 237 samples; 78.1%).

Our final network had 281 phylotypes and was arranged into 10 ecological clusters. Among these clusters, we identified three major groups of co-occurring taxa and composing 65% of the

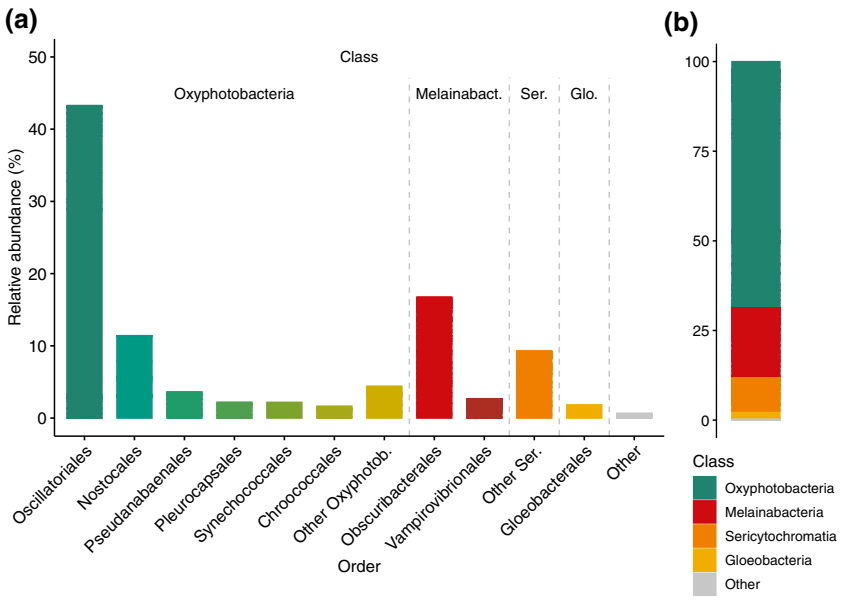

FIGURE 1 Taxonomic information on the relative abundance of cyanobacterial orders (a) and classes (b) across all sites. Glo. = Gloeobacteria; Melainabact. = Melainabacteria; Ser. = Sericytochromatia (no orders described yet) [Colour figure can be viewed at wileyonlinelibrary.com]

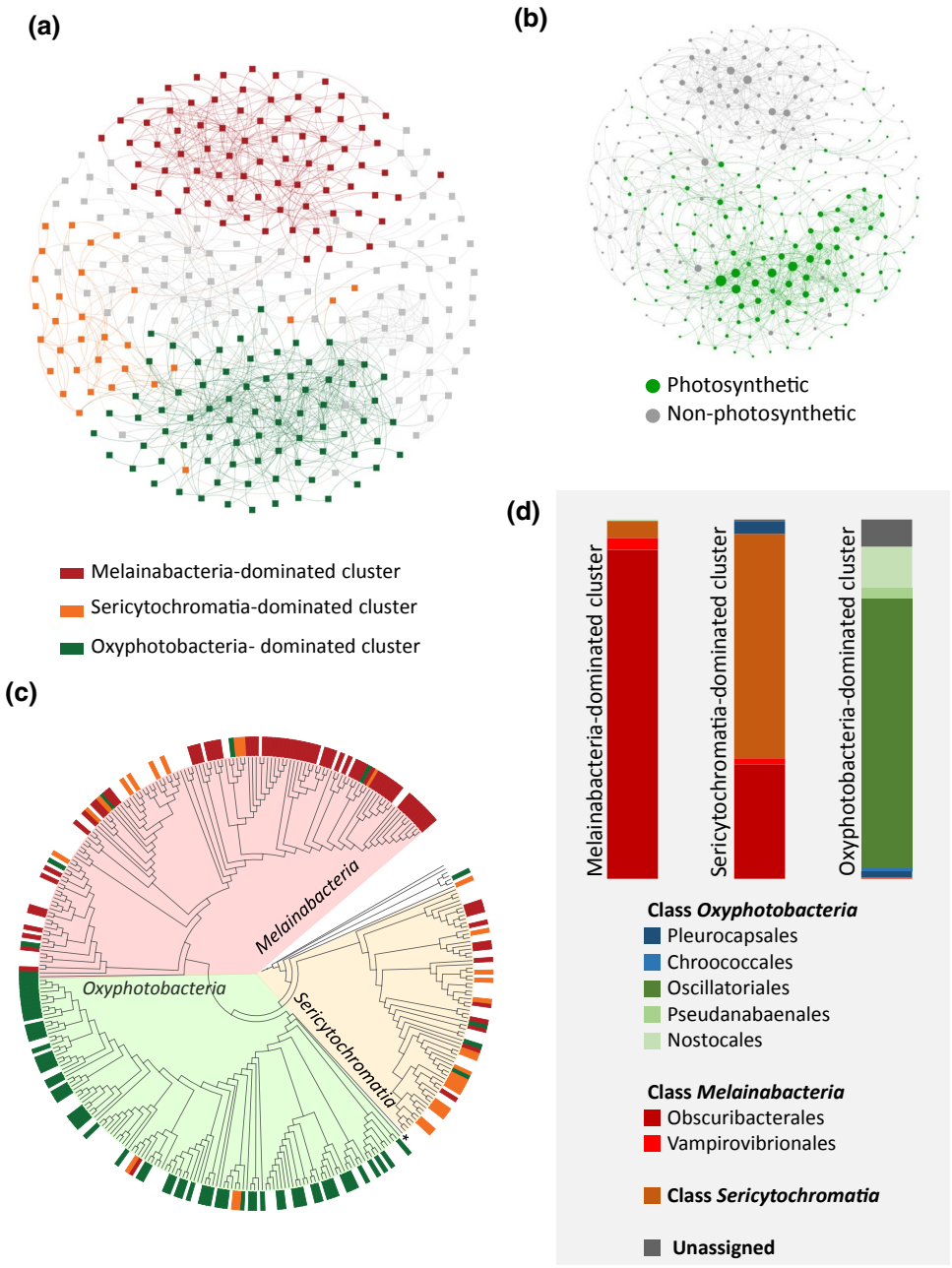

FIGURE 2 Global network of co-occurrences within soil cyanobacteria, coloured by either main ecological clusters (a) or the photosynthetic capability of taxa (b). The size of the nodes is related to the number of links they contain. The network had 282 nodes (cyanobacterial phylotypes) and 986 significant links (potential ecological interactions between phylotypes). (c) Phylogenetic tree obtained with the main ecological clusters located at the end of the branch. Background is coloured by cyanobacterial class; * for Gloeobacteria class. (d) Taxonomic composition in relation to total 16S reads [Colour figure can be viewed at wileyonlinelibrary.com]

cyanobacterial phylotypes identified (Figure 2a). The remaining seven clusters were minor, encompassing between 8 and 1% of phylotypes. The three main ecological clusters were dominated by Oxyphotobacteria (82% of 76 phylotypes), Sericytochromatia (52% of 31 phylotypes) or Melainabacteria (83% of 76 phylotypes; see Supporting Information Table S1). We focused on these main ecological clusters for the downstream analyses. Our correlation network showed a contrasting node distribution for cyanobacterial phylotypes characterized by photosynthetic and non-photosynthetic capabilities (Figure 2b). Overall, the three ecological clusters identified were strongly dominated by the three extant cyanobacterial classes (Figure 2c,d).

3.2 | Environmental preferences of photosynthetic and non-photosynthetic soil cyanobacteria

Vegetation type significantly affected the abundance of each of the main cyanobacterial clusters identified (PERMANOVA R^2 = 0.28, 0.24 and

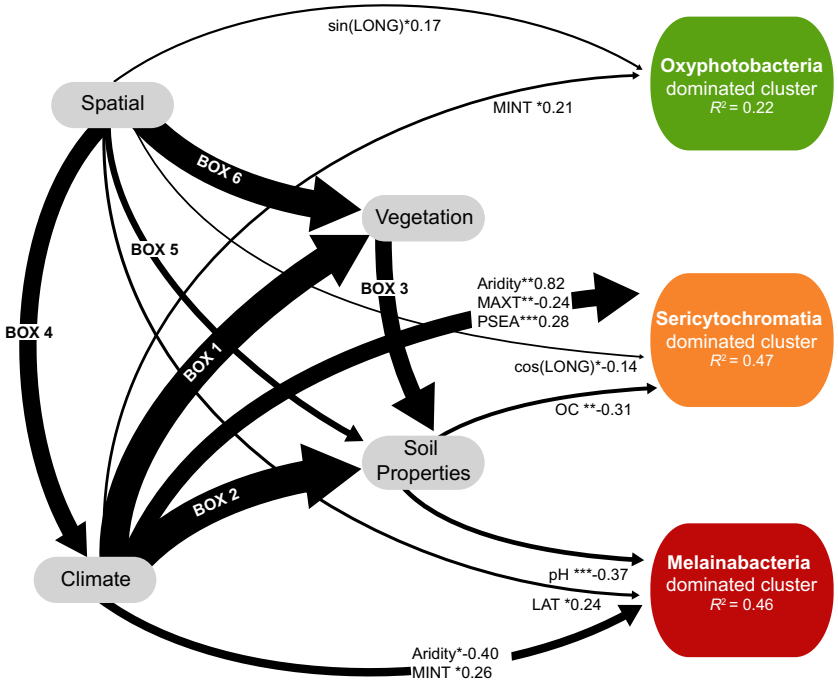

FIGURE 3 Structural equation model showing the direct effects of spatial {latitude [LAT], sine longitude [sin(LONG)] and cosine longitude [cos(LONG)]}, climatic [maximum temperature (MAXT), minimum temperature (MINT), precipitation seasonality (PSEA) and aridity, calculated as 1 − aridity index] and soil [soil organic carbon (OC) and pH] variables on the abundance of each ecological cluster. Numbers associated with arrows indicate standardized path coefficients, and the arrow width is proportional to the strength of path coefficients. The proportion of variance explained (R^2) appears below every response variable in the model. Significance levels are as follows $^*p < .05$, $^{**}p < .01$ and $^{***}p < .001$. Model $\chi^2 = 2.567$, $p = .463$, d.f. = 3; bootstrap $p = .254$. Information on boxes 1–6 is shown in the Supporting Information (Figure S2) [Colour figure can be viewed at wileyonlinelibrary.com]

0.15 for Melainabacteria-, Sericytochromatia- and Oxyphotobacteria-dominated clusters, respectively; $p < .05$ in all cases).

Our structural equation model indicated that the cluster dominated by Oxyphotobacteria was positively and negatively related to aridity and net aboveground productivity, respectively (Figures 3 and 4; Supporting Information Figure S4a), which explains their high relative abundance in dry grasslands (Figure 5). We also observed a positive association between the relative abundance of the Oxyphotobacteria-dominated cluster and both soil pH and minimum temperature (Figures 3 and 4; Supporting Information Figure S4a). We predicted the distribution of this cluster in a wide range of arid and semi-arid areas worldwide (e.g., southern Sahara, southern Africa, northern Australia, India, Arabian Peninsula, areas surrounding the Amazon Basin, southwestern USA and northwestern Mexico; Figure 6a).

The cluster dominated by Sericytochromatia had a strong preference for arid environments with low soil C content (Figures 3, 4 and 5; Supporting Information Figure S4b). Taxa within this ecological cluster were also positively associated with locations characterized by high inter-annual rainfall variability (Figures 3 and 4; Supporting Information Figure S4b). Our global atlas predicts that taxa within this ecological cluster can be found in hyper-arid areas, such as the Saharan Desert, central Australia, the Atacama, Gobi and Taklamakan Deserts and the Arabian Peninsula, with almost no areas of intermediate relative abundance (Figure 6).

Unlike the other two ecological clusters identified, the Melainabacteria-dominated cluster showed a preference for humid and acidic soils, as indicated by the reduced relative abundance of this cluster with increases in aridity and pH (Figures 3 and 4; Supporting Information Figure S4c). The vast majority of phylotypes found in our study corresponded to the order Obscuribacterales (Figures 1 and 2d). This ecological cluster is found mainly in tropical and cold forests and grasslands (which are mostly temperate; see Figure 5). Prediction maps show high relative abundance values of this cluster in humid areas of the Amazon Basin, central Africa, the west Asian coast and Pacific Islands (Figure 6). Despite the methodological differences between our dataset and the EMP dataset (primer sets used here 341F/805R vs. 515F/806R for the EMP; read lengths here 400 bp/sequence vs. <150 bp for the EMP, and the lack of standardization in the EMP soil sampling protocols and metadata collection), we obtained positive and significant correlations between both results: Melainabacteria-dominated cluster, Pearson's $r = 0.28$ ($p < .001$); Sericytochromatia-dominated cluster, Pearson's $r = 0.53$ ($p < .001$); and Oxyphotobacteria-dominated cluster Pearson's $r = 0.35$ ($p < .001$). These results support the validity of our maps as representative of the distribution of the main ecological clusters of cyanobacteria across the globe.

4 | DISCUSSION

The discovery of non-photosynthetic cyanobacteria has expanded one of the currently most diverse bacterial phylum

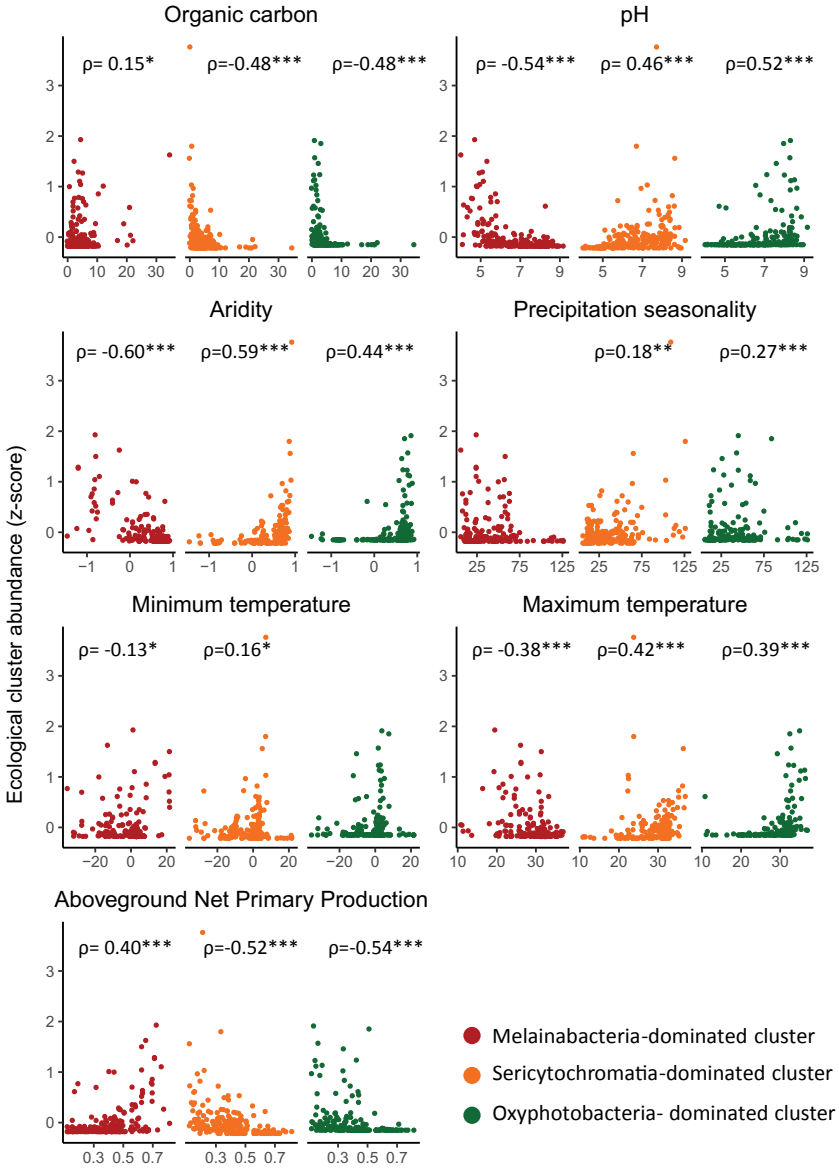

FIGURE 4 Relationships between main environmental predictors and the relative abundance (*z*-score) of each one of the cyanobacterial clusters. Significant ($p < .05$) Spearman correlation coefficients are shown in the upper part of each panel [Colour figure can be viewed at wileyonlinelibrary.com]

(Castenholz et al., 2001; Dvořák et al., 2017; Garcia-Pichel, 2009; Whitton & Potts, 2012). There is a large body of knowledge about photosynthetic cyanobacteria showing their importance in terrestrial ecosystems, because they are key components of cryptogamic covers, which are estimated to fix 3.9 Pg carbon/year (Elbert et al., 2012). They increase soil fertility by fixing atmospheric N (Cleveland et al., 1999) and stabilize soils by producing extracellular polysaccharides (Mager & Thomas, 2011; Mazor, Kidron, Vonshak, & Abeliovich, 1996), protecting it from erosion and creating suitable habitats for the colonization of mosses and lichens (Lan, Wu, Zhang, & Hu, 2015; Zhang, 2005). However, we know relatively little about the distribution and environmental drivers of the newly described non-photosynthetic cyanobacteria in soils. Our work provides new insights into the ecology and biogeography of these key organisms and advances our understanding of on the potential vulnerabilities of photosynthetic and non-photosynthetic cyanobacteria to changing environmental conditions.

Photosynthetic taxa represented by the Oxyphotobacteria-dominated cluster prefer areas with sparse vegetation cover and, therefore, greater accessibility to light, such as dry grasslands (Figures 3, 4 and 5; Supporting Information Figure S4a). Accordingly, they are reported as key components of biocrust communities in low-productivity ecosystems, such as arid environments (Belnap, Weber, & Büdel, 2016; Garcia-Pichel, 2009), where the ability to fix atmospheric C and N can be an important ecological advantage. As with the remaining bacterial communities (Fierer & Jackson, 2006), soil acidity is a key factor shaping the global distribution of Oxyphotobacteria (Figure 4). Consistent with previous studies (Baas-Becking, Kaplan, & Moore, 1960; Brock, 1973; Nayak & Prasanna, 2007), we found that photosynthetic cyanobacteria have a preference for neutral to alkaline soils (Figures 3 and 4; Supporting Information Figure S4a), which are characteristic of drylands (Schlesinger & Bernhardt, 2013). Our analyses also indicate a wide distribution of this cluster in drylands worldwide (Figure 5), as reported previously for members

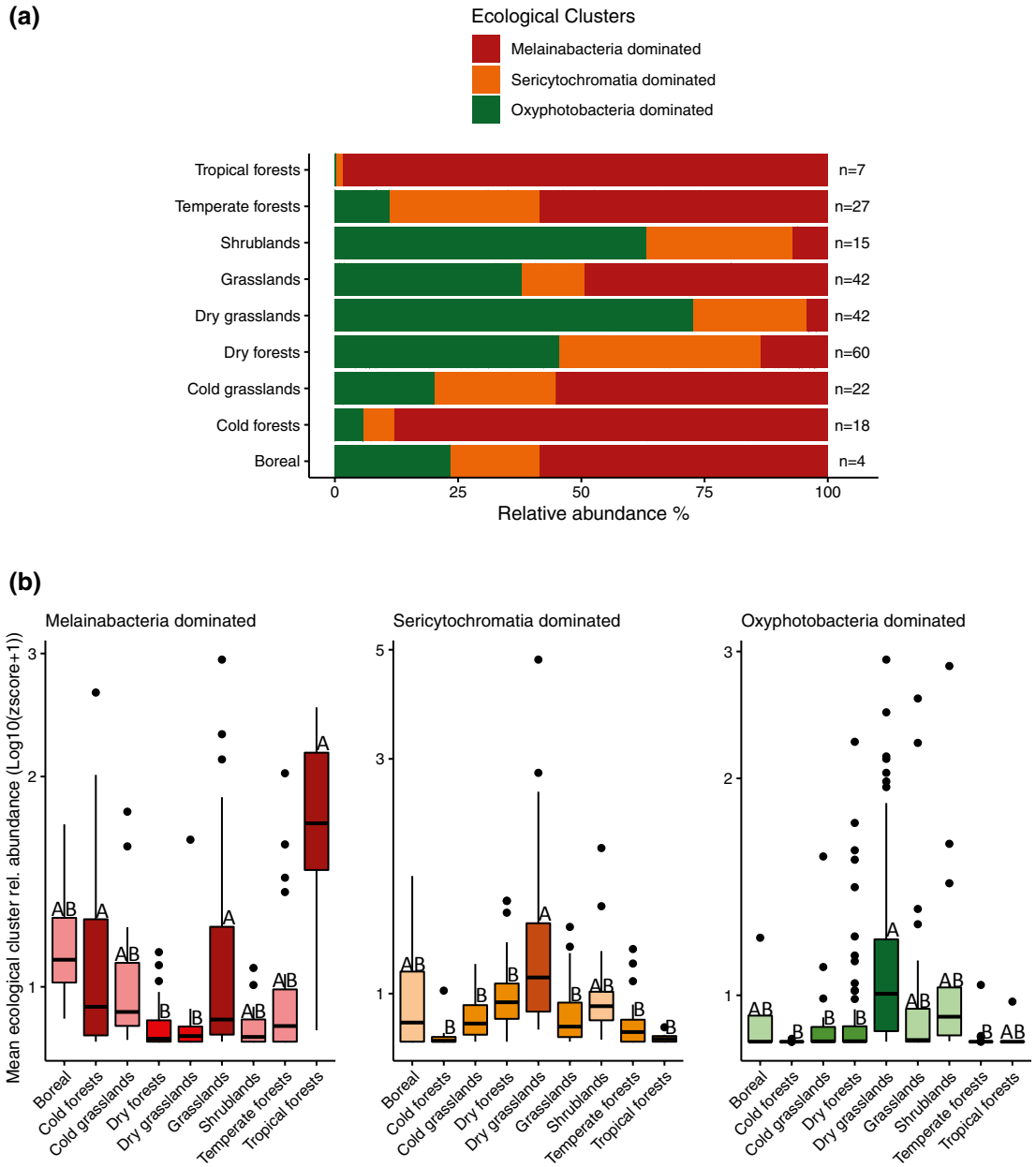

FIGURE 5 Relative abundance of cyanobacterial clusters across major vegetation types. (a) Stacked bars showing the percentage of phylotypes of each ecological cluster per vegetation type. *n* = number of sites for each vegetation type. (b) Tukey's HSD test results for the differences (letters and colour hues) in the relative abundances of each ecological cluster across vegetation types [Colour figure can be viewed at wileyonlinelibrary.com]

of this taxa in continental-scale distribution studies (Bahl et al., 2011; Garcia-Pichel, Loza, Marusenko, Mateo, & Potrafka, 2013). Together with temperature, soil moisture plays a key role driving the physiology, small-scale distribution and behaviour of soil photosynthetic cyanobacteria (Garcia-Pichel & Pringault, 2001; Rajeev et al., 2013). The high tolerance and photosynthetic performance of Oxyphotobacteria at high temperatures is one of the reasons why cyanobacterial-dominated biocrusts are so abundant in hyper-arid and arid environments (Grote, Belnap, Housman, & Sparks, 2010; Wang, Wang, Shu, & Zhang, 2013). Thus, we observed a positive influence of high minimum temperatures and aridity on this cyanobacterial cluster (Figure 3; Supporting Information Figure S4a). By moving from the local/regional scale to the global scale, including samples from poorly studied regions of South America (Büdel et al., 2016; Garcia-Pichel et al., 2003) and considering multiple terrestrial global biomes, our results provide new predictions of the global distribution of Oxyphotobacteria in global soils.

Unlike Oxyphotobacteria, non-photosynthetic cyanobacteria require relatively large soil organic C pools for growth. We observed contrasting environmental preferences for each of the non-photosynthetic clusters across the oligotrophic–copiotrophic continuum,

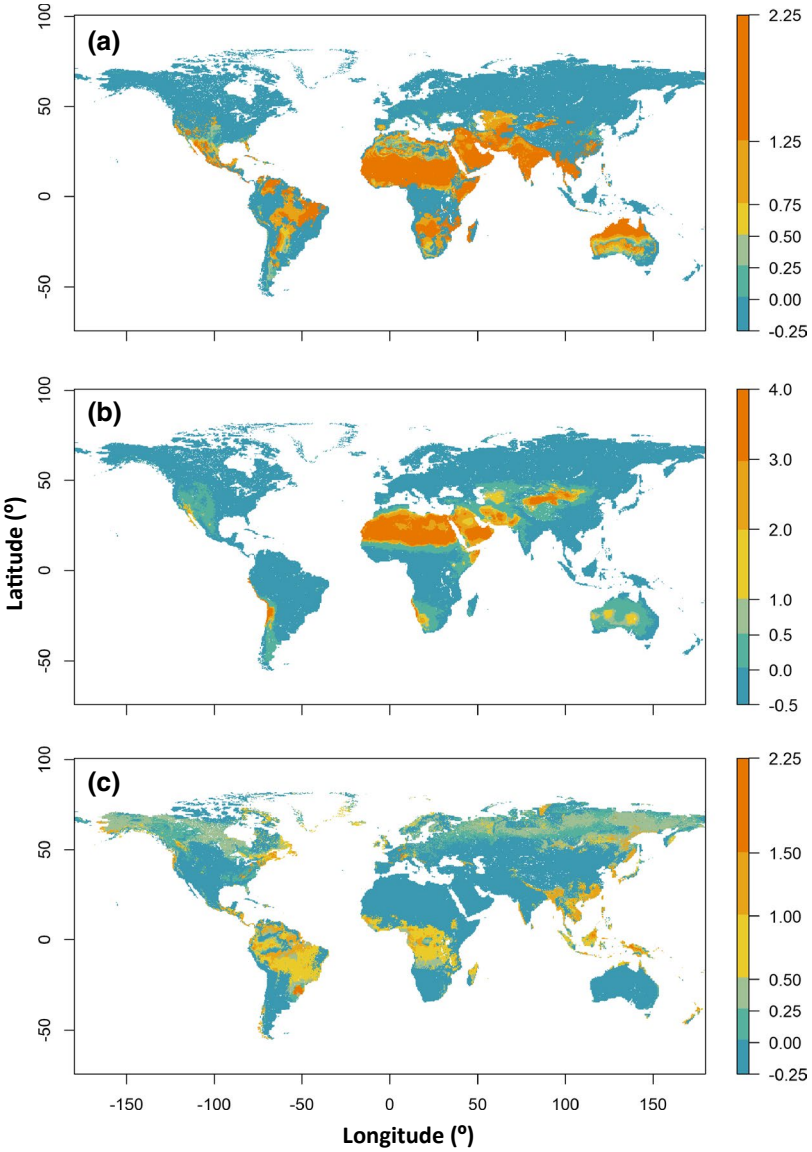

FIGURE 6 Predicted global distribution of the relative abundance of the main ecological clusters of soil cyanobacteria. The percentage of variation explained by the models is as follows: (a) Oxyphotobacteria-dominated cluster, $R^2 = 0.28$; $p < .001$; (b) Sericytochromatia-dominated cluster, $R^2 = 0.66$; $p < .001$; and (c) Melainabacteria-dominated cluster, $R^2 = 0.35$; $p < .001$. The scale bar represents the standardized abundance (*z*-score) of each ecological cluster. An independent cross-validation for these maps using data from the Earth Microbiome Project (Thompson et al., 2017) is described in the Materials and Methods section [Colour figure can be viewed at wileyonlinelibrary.com]

such as those reported for other soil heterotrophic organisms (e.g., methanotrophs, by Nazaries et al. (2018)). A key finding of our study is that the Melainabacteria-dominated cluster is especially abundant in mesic forests (tropical and cold forests; Figure 6) and temperate grasslands, whereas the Sericytochromatia-dominated cluster is associated with locations with reduced plant cover and high temperatures (e.g., hyper-arid deserts in Figure 5; dry grasslands in Figure 6). We found very little overlap between the predicted distributions of non-photosynthetic clusters of cyanobacteria (Figure 6) and a negative relationship between the relative abundances of these two non-photosynthetic clusters (Spearman's correlation $r = -0.31$, $p < .05$). Interestingly, a sizeable percentage of members of Melainabacteria appears in the Sericytochromatia-dominated cluster (38%). We know that members of class Melainabacteria are capable of aerobic respiration because they contain respiratory components of the complex III–IV operon, which is adapted to low-oxygen conditions, a C-family oxygen reductase and two cytochrome *bc* oxidases (Soo et al., 2017). However, the Melainabacteria-dominated cluster is dominated by members of the order Obscuribacterales (Figure 2d), for which there is little functional information available in the literature. Genomic analyses of *Obscuribacter phosphatis* suggest that this particular species is adapted to dynamic environments involving feast–famine nutrient cycles and has the capacity for aerobic or anaerobic respiration and fermentation (Soo et al., 2014). These features allow it to survive in both oxic and anoxic environments. To our knowledge, there is no information available on the contribution of this cyanobacterium to the structure and function of forest ecosystems. However, our results suggest that molecular ecologists and taxonomists targeting taxa in the Melainabacteria-dominated cluster should focus mainly on mesic forests across the globe. We also expect non-photosynthetic cyanobacteria to play a significant role in soil biogeochemical cycles in both high and low productive soils through C degradation and/or hydrogen production, as reported for Melainabacteria in an alluvial aquifer (Wrighton et al., 2014).

However, studies linking non-photosynthetic soil cyanobacteria to carbon degradation in terrestrial environments are still lacking. Future studies are thus needed to identify the relative contributions of non-photosynthetic cyanobacteria to decomposition of organic matter and C cycling in soils from contrasting biomes.

The topology of our phylogenetic tree (Figure 2c) reflects the expected evolutionary relationships from previous research, with separation of three main clades (Soo et al., 2017); the basal deep branched Sericytochromatia, Melainabacteria and photosynthetic Oxyphotobacteria. Given that the ecological clusters are related to these classes, their global distribution is likely to be related to past evolutionary events within this ancient phylum (Bahl et al., 2011; Moreira et al., 2013). The ecological diversification observed in the non-photosynthetic clades is particularly noteworthy. We found a niche differentiation between the basal cyanobacterial clade, Sericytochromatia, which occupies extremely dry environments, and Melainabacteria, which is mostly found in humid forests. Interestingly, the presence of phylotypes from Melainabacteria in the Sericytochromatia-dominated cluster might point to the existence of common ancestral traits between both classes and the later expansion of Melainabacteria into new "humid" niches. Photosynthetic cyanobacteria (Oxyphotobacteria) are known for their extraordinary ecological versatility, living mostly in environments with at least some exposure to sunlight and being capable of inactivating their photosynthetic apparatus (Harel, Ohad, & Kaplan, 2004) or performing light-independent energy generation (Stal, 2012) when needed. There is still no consensus about the date for acquisition of oxygenic photosynthesis by Oxyphotobacteria; this could have happened either after divergence from other non-photosynthetic clades (Soo et al., 2017) or before, sharing a photosynthetic common ancestor (Harel et al., 2015). Regardless, the acquisition of oxygenic photosynthesis was a revolutionary event that allowed cyanobacteria to expand into diverse niches, in addition to the evolution of algae and terrestrial plants through endosymbiosis (Margulis, 1970; Mereschkowsky, 1905).

Our findings represent a starting point for the understanding of the ecological preferences and global distributions of non-photosynthetic soil cyanobacteria. They highlight the fact that major photosynthetic and non-photosynthetic groups of soil cyanobacteria have contrasting ecological preferences across the globe. However, and given the difficulty of predicting microorganisms at a global scale, conclusions should be viewed as preliminary. The potential distribution maps presented here and the identification of the main environmental drivers of soil cyanobacterial distribution also illustrate how different cyanobacterial lineages might respond to ongoing changes in climate and land use. For example, the positive influence of aridity on the Sericytochromatia- and Oxyphotobacteria-dominated clusters suggests that the distribution of these taxa could expand under future climate change scenarios (Huang, Yu, Guan, Wang, & Guo, 2016). Consequently, our findings advance our understanding of the ecological distributions of these functionally important microbial communities and provide a basis for predicting possible future shifts of cyanobacterial terrestrial communities in a human-dominated, warmer and more arid world. To complement and expand our findings, future studies should investigate further the temporal dynamics of photosynthetic and non-photosynthetic cyanobacteria in terrestrial ecosystems, particularly on multiple temporal scales.

ACKNOWLEDGMENTS

We would like to thank Victoria Ochoa and Beatriz Gozalo for their help with soil analyses and Hugo Saiz for his help with network analyses. We are grateful to Christophe V. W. Seppey and the two anonymous reviewers for their insightful comments and suggestions. M.D.-B. is supported by a Ramón y Cajal grant from the Spanish Ministry of Science and Innovation (RYC2018-025483-I), and by the BES grant agreement No LRB17\1019 (MUSGONET). The work of C.C.-D. and F.T.M. and the global drylands database were supported by the European Research Council [ERC Grant Agreements 242658 (BIOCOM) and 647038 (BIODESERT)] and by the Spanish Ministry of Economy and Competitiveness (BIOMOD project, ref. CGL2013-44661-R). F.T.M. acknowledges support from Generalitat Valenciana (BIOMORES project, ref. CIDEGENT/2018/041). Research on biodiversity by B.K.S. is supported by the Australian Research Council (DP170104634). R.D.B. was supported by the U.K. Department of Environment, Food and Rural Affairs (DEFRA) project no. BD5003 and a Biotechnology and Biological Sciences Research Council (BBSRC) International Exchange Grant (BB/L026406/1).

DATA AVAILABILITY STATEMENT

Raw data related to this manuscript are available in Figshare, https://figshare.com/s/82a2d3f5d38ace925492

ORCID

Concha Cano-Díaz https://orcid.org/0000-0001-6948-6553
Fernando T. Maestre https://orcid.org/0000-0002-7434-4856
David J. Eldridge https://orcid.org/0000-0002-2191-486X
Brajesh K. Singh https://orcid.org/0000-0003-4413-4185
Richard D. Bardgett https://orcid.org/0000-0002-5131-0127
Noah Fierer https://orcid.org/0000-0002-6432-4261
Manuel Delgado-Baquerizo https://orcid.org/0000-0002-6499-576X

REFERENCES

Adams, D. G., & Duggan, P. S. (1999). Heterocyst and akinete differentiation in cyanobacteria. *New Phytologist*, *144*, 3–33.

Baas-Becking, L. G. M., Kaplan, I. R., & Moore, D. (1960). Limits of the natural environment in terms of pH and oxidation-reduction potentials. *The Journal of Geology*, *68*, 243–284.

Bahl, J., Lau, M. C. Y., Smith, G. J. D., Vijaykrishna, D., Cary, S. C., Lacap, D. C., … Pointing, S. B. (2011). Ancient origins determine global biogeography of hot and cold desert cyanobacteria. *Nature Communications*, *2*, 161–166.

Bastian, M., Heymann, S., & Jacomy, M. (2009). Gephi: an open source software for exploring and manipulating networks. *Proceedings of the 3rd International ICWSM Conference*, *8*, 361–362.

Belnap, J., Weber, B., & Büdel, B. (2016). Chapter 1: Biological soil crusts as an organizing principle in drylands. *Biological soil crusts as an organizing principle in drylands*, Ecological Studies (*226*, pp. 3–13). Cham, Switzerland: Springer International Publishing.

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, *57*, 289–300.

Billi, D., Friedmann, E. I., Hofer, K. G., & Caiola, M. G. (2000). Ionizing-radiation resistance in the desiccation-tolerant cyanobacterium *Chroococcidiopsis*. *Applied and Environmental Microbiology*, *66*, 1489–1492.

Bontemps, S., Defourny, P., Radoux, J., Van Bogaert, E., Lamarche, C., Achard, F., … Arino, O. (2013). Consistent global land cover maps for climate modeling communities: Current achievements of the ESA's land cover CCI. *Proceedings of the ESA Living Planet Symposium, Edimburgh*. 9–13.

Brock, T. D. (1973). Lower pH limit for the existence of blue-green algae: Evolutionary and ecological implications. *Science*, *179*, 480–483.

Büdel, B., Dulić, T., Darienko, T., Rybalka, N., & Friedl, T. (2016). Chapter 4: Cyanobacteria and algae of biological soil crusts. In B. Weber, B. Büdel, & J. Belnap (Eds.), *Biological soil crusts: An organizing principle in drylands*, Ecological Studies (*226*, pp. 55–80). Cham, Switzerland: Springer International Publishing.

Caporaso, J. G., Kuczynski, J., Stombaugh, J., Bittinger, K., Bushman, F. D., Costello, E. K., … Knight, R. (2010). QIIME allows analysis of high-throughput community sequencing data. *Nature Methods*, *7*, 335–336.

Carini, P., Delgado-Baquerizo, M., Hinckley, E. S., Brewer, T. E., Rue, G., Vanderburgh, C., Mcknight, D., & Fierer, N. (2020). Effects of spatial variability and relic DNA removal on the detection of temporal dynamics in soil microbial communities. *Ecological and Evolutionary Science*, *11*, e02776-19.

Castenholz, R. W., Wilmotte, A., Herdman, M., Rippka, R., Waterbury, J. B., Iteman, I., & Hoffmann, L. (2001). Phylum BX. Cyanobacteria. In D. R. Boone, R. W. Castenholz, & G. M. Garrity (Eds.), *Bergey's manual of systematic bacteriology. Volume One: The Archaea and the deeply branching and phototrophic bacteria* (pp. 473–599). New York, NY: Springer New York.

Cleveland, C. C., Townsend, A. R., Schimel, D. S., Fisher, H., Hedin, L. O., Perakis, S., … Wasson, M. F. (1999). Global patterns of terrestrial biological nitrogen (N_2) fixation in natural ecosystems. *Global Biogeochemical Cycles*, *13*, 623–645.

Csárdi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal Complex Systems*, *1695*, 1–9.

Delgado-Baquerizo, M., Oliverio, A. M., Brewer, T. E., Benavent-González, A., Eldridge, D. J., Bardgett, R. D., … Fierer, N. (2018). A global atlas of the dominant bacteria found in soil. *Science*, *325*, 320–325.

DeSantis, T. Z., Hugenholtz, P., Larsen, N., Rojas, M., Brodie, E. L., Keller, K., … Andersen, G. L. (2006). Greengenes, a chimera-checked 16S rRNA gene database and workbench compatible with ARB. *Applied and Environmental Microbiology*, *72*, 5069–5072.

Di Rienzi, S. C., Sharon, I., Wrighton, K. C., Koren, O., Hug, L. A., Thomas, B. C., … Ley, R. E. (2013). The human gut and subsurface harbor non-photosynthetic Cyanobacteria. *eLife*, *2*, e01102.

Dismukes, G. C., Klimov, V. V., Baranov, S. V., Kozlov, Y. N., DasGupta, J., & Tyryshkin, A. (2001). The origin of atmospheric oxygen on Earth: The innovation of oxygenic photosynthesis. *Proceedings of the National Academy of Sciences USA*, *98*, 2170–2175.

Domínguez, S. G., & Asencio, A. D. (2011). Distribution of chasmoendolithic cyanobacteria in gypsiferous soils from semi-arid environments (SE Spain) by chemical and physical parameters. *Nova Hedwigia*, *92*, 1–27.

Dvořák, P., Casamatta, D. A., Hašler, P., Jahodářová, E., Norwich, A. R., & PoPoulíčková, A. (2017). Diversity of the cyanobacteria. In P. C. Hallenbeck (Ed.), *Modern topics in the phototrophic prokaryotes: Environmental and applied aspects* (pp. 3–46). Cham, Switzerland: Springer International Publishing.

Dvořák, P., Hašler, P., & Poulíčková, A. (2012). Phylogeography of the *Microcoleus vaginatus* (Cyanobacteria) from three continents – A spatial and temporal characterization. *PLoS ONE*, *7*, e40153.

Edgar, R. C. (2010). Search and clustering orders of magnitude faster than BLAST. *Bioinformatics*, *26*, 2460–2461.

Edgar, R. C. (2013). UPARSE: Highly accurate OTU sequences from microbial amplicon reads. *Nature Methods*, *10*, 996–998.

Elbert, W., Weber, B., Burrows, S., Steinkamp, J., Büdel, B., Andreae, M. O., & Pöschl, U. (2012). Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. *Nature Geoscience*, *5*, 459–462.

Faust, K., & Raes, J. (2012). Microbial interactions: From networks to models. *Nature Reviews Microbiology*, *10*, 538–550.

Faust, K., & Raes, J. (2016). CoNet app: inference of biological association networks using Cytoscape. *F1000Research*, *5*, 1519.

Fierer, N., & Jackson, R. B. (2006). The diversity and biogeography of soil bacterial communities. *Proceedings of the National Academy of Sciences USA*, *103*, 626–631.

Flombaum, P., Gallegos, J. L., Gordillo, R. A, Rincón, J., Zabala, L. L., Jiao, N., … Martiny, A. C. (2013). Present and future global distributions of the marine Cyanobacteria *Prochlrococcus* and *Synechococcus*. *Proceedings of the National Academy of Sciences USA*, *110*, 9824–9829.

Garcia-Pichel, F. (2009). Cyanobacteria. In T. M. Schmidt (Ed.), *Encyclopedia of microbiology*, 4th ed., (pp. 107–124). San Diego: Academic Press.

Garcia-Pichel, F., Belnap, J., Neuer, S., & Schanz, F. (2003). Estimates of global cyanobacterial biomass and its distribution. *Algological Studies*, *109*, 213–227.

Garcia-Pichel, F., López-Cortés, A., & Nübel, U. (2001). Phylogenetic and morphological diversity of cyanobacteria in soil desert crusts from the Colorado Plateau. *Applied and Environmental Microbiology*, *67*, 1902–1910.

Garcia-Pichel, F., Loza, V., Marusenko, Y., Mateo, P., & Potrafka, R. M. (2013). Temperature drives the continental-scale distribution of key microbes in topsoil communities. *Science*, *340*, 1574–1577.

Garcia-Pichel, F., & Pringault, O. (2001). Cyanobacteria track water in desert soils. *Nature*, *413*, 380–381.

Garcia-Pichel, F., Prufert-Bebout, L., & Muyzer, G. (1996). Phenotypic and phylogenetic analyses show *Microcoleus chthonoplastes* to be a cosmopolitan cyanobacterium. *Applied and Environmental Microbiology*, *62*, 3284–3291.

Grace, J. B. (2006). *Structural equation modeling and natural systems*, New York, NY: Cambridge University Press.

Grote, E. E., Belnap, J., Housman, D., & Sparks, J. P. (2010). Carbon exchange in biological soil crust communities under differential temperatures and soil water contents : implications for global change. *Global Change Biology*, *16*, 2763–2774.

Harel, A., Karkar, S., Falkowski, P. G., Harel, A., Karkar, S., & Cheng, S. (2015). Deciphering primordial cyanobacterial genome functions from protein network analysis. *Current Biology*, *25*, 628–634.

Harel, Y., Ohad, I., & Kaplan, A. (2004). Activation of photosynthesis and resistance to photoinhibition in cyanobacteria within biological desert crust. *Plant Physiology*, *136*, 3070–3079.

Hengl, T., Mendes de Jesus, J., Heuvelink, G. B. M., Ruiperez Gonzalez, M., Kilibarda, M., Blagotić, A., … Kempen, B. (2017). SoilGrids250m: Global gridded soil information based on machine learning. *PLoS ONE*, *12*, e0169748.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*, 1965–1978.

Huang, J., Yu, H., Guan, X., Wang, G., & Guo, R. (2016). Accelerated dryland expansion under climate change. *Nature Climate Change*, *6*, 166–171.

Jungblut A. D., Lovejoy C., & Vincent W. F. (2010). Global distribution of cyanobacterial ecotypes in the cold biosphere. *The ISME Journal*, *4*(2), 191–202. http://dx.doi.org/10.1038/ismej.2009.113

Justice, C. O., Vermote, E., Defries, R., & Roy, D. P. (1998). The Moderate Resolution Imaging Spectroradiometer (MODIS): Land remote sensing for global change research. *IEEE Transactions on Geoscience and Remote Sensing*, *36*, 1228–1249.

Kellogg, C. A., & Griffin, D. W. (2006). Aerobiology and the global transport of desert dust. *Trends in Ecology and Evolution*, *21*, 638–644.

Kuhn, M., Weston, S., Keefer, C., Coulter, N., & Quinlan, R. (2016). Cubist: Rule-and instance-based regression modeling. R package version 0.0.19.

Lan, S., Wu, L., Zhang, D., & Hu, C. (2015). Analysis of environmental factors determining development and succession in biological soil crusts. *Science of the Total Environment*, *538*, 492–499.

Letunic, I., & Bork, P. (2019). Interactive Tree Of Life (iTOL) v4: Recent updates and new developments. *Nucleic Acids Research*, *47*, W256–W259.

Ley, R. E., Backhed, F., Turnbaugh, P., Lozupone, C. A., Knight, R. D., & Gordon, J. I. (2005). Obesity alters gut microbial ecology. *Proceedings of the National Academy of Sciences USA*, *102*, 11070–11075.

Li, R., Tun, H. M., Jahan, M., Zhang, Z., Kumar, A., Fernando, D., Farenhorst, A., & Khafipour, E. (2017). Comparison of DNA-, PMA-, and RNA-based 16S rRNA Illumina sequencing for detection of live bacteria in water. *Scientific Reports*, *7*, 5752.

Lund, J. W. G. (1967). Soil algae. In A. Burges & F. Raw (Eds.), *Soil biology* (pp. 129–147). London and New York: Academic Press.

Maestre, F. T., Delgado-Baquerizo, M., Jeffries, T. C., Eldridge, D. J., Ochoa, V., Gozalo, B., … Singh, B. K. (2015). Increasing aridity reduces soil microbial diversity and abundance in global drylands. *Proceedings of the National Academy of Sciences USA*, *112*, 15684–15689.

Mager, D. M., & Thomas, A. D. (2011). Extracellular polysaccharides from cyanobacterial soil crusts: A review of their role in dryland soil processes. *Journal of Arid Environments*, *75*, 91–97.

Margulis, L. (1970). *Origin of eukaryotic cells: Evidence and research implications for a theory of the origin and evolution of microbial, plant and animal cells on the Precambrian Earth*, New Haven-London: Yale University Press.

Mazor, G., Kidron, G. J., Vonshak, A., & Abeliovich, A. (1996). The role of cyanobacterial exopolysaccharides desert microbial crusts. *FEMS Microbiology Ecology*, *21*, 121–130.

Mereschkowsky, C. (1905). Uber Natur und Ursprung der Chromatophoren im Pflanzenreiche. *Biologisches Centralblatt*, *25*, 293–604.

Monchamp, M., Spaak, P., Domaizon, I., Dubois, N., Bouffard, D., & Pomati, F. (2018). Homogenization of lake cyanobacterial communities over a century of climate change and eutrophication. *Nature Ecology and Evolution*, *2*, 317–324.

Monchamp, M., Spaak, P., & Pomati, F. (2019). Long term diversity and distribution of non-photosynthetic Cyanobacteria in peri-Alpine lakes. *Frontiers in Microbiology*, *9*, 3344.

Moreira, C., Vasconcelos, V., & Antunes, A. (2013). Phylogeny and biogeography of Cyanobacteria and their produced toxins. *Marine Drugs*, *11*, 4350–4369.

Namsaraev, Z., Mano, M. J., Fernandez, R., & Wilmotte, A. (2010). Biogeography of terrestrial cyanobacteria from Antarctic ice-free areas. *Annals of Glaciology*, *51*, 171–177.

Nayak, S., & Prasanna, R. (2007). Soil pH and its role in cyanobacterial abundance and diversity in rice field soils. *Applied Ecology and Environmental Research*, *5*, 103–113.

Nazaries, L., Karunaratne, S. B., Delgado-Baquerizo, M., Campbell, C. D., & Singh, B. K. (2018). Environmental drivers of the geographical distribution of methanotrophs: Insights from a national survey. *Soil Biology and Biochemistry*, *127*, 264–279.

Nei, M., & Kumar, S. (2000). *Molecular evolution and phylogenetics*, New York: Oxford University Press.

Newman, P. A., & McKenzie, R. (2011). UV impacts avoided by the Montreal Protocol. *Photochemical & Photobiological Sciences*, *10*, 1152–1160.

Oksanen, J. (2015). Vegan: an introduction to ordination. Retrieved from http://cran.r-project.org/web/packages/vegan/vignettes/introvegan.pdf, **8**, 19.

Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J. M., Tucker, C. J., & Stenseth, N. C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology and Evolution*, *20*, 503–510.

Price, M. N., Dehal, P. S., & Arkin, A. P. (2009). Fasttree: Computing large minimum evolution trees with profiles instead of a distance matrix. *Molecular Biology and Evolution*, *26*, 1641–1650.

Pruesse, E., Peplies, J., & Glöckner, F. O. (2012). SINA: Accurate high-throughput multiple sequence alignment of ribosomal RNA genes. *Bioinformatics*, *28*, 1823–1829.

Puente-Sánchez, F., Arce-Rodríguez, A., Oggerin, M., García-Villadangos, M., Moreno-Paz, M., Blanco, Y., … Amils, R. (2018). Viable cyanobacteria in the deep continental subsurface. *Proceedings of the National Academy of Sciences USA*, *115*, 10702–10707.

Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., & Glöckner, F. O. (2013). The SILVA ribosomal RNA gene database project: Improved data processing and web-based tools. *Nucleic Acids Research*, *41*, 590–596.

Quesada, A., & Vincent, W. F. (2012). Cyanobacteria in the cryosphere: snow, ice and extreme cold. In B. A. Whitton (Ed.), *Ecology of cyanobacteria II* (pp. 387–399). Dordrecht: Springer.

Quinlan, J. R. (2014). *C4.5: Programs for machine learning*, Mateo, CA: Elsevier.

R Core Team. (2013). R: A language and environment for statistical computing.

Rajeev, L., Nunes, U., Klitgord, N., Luning, E. G., Fortney, J., Axen, S. D., … Mukhopadhyay, A. (2013). Dynamic cyanobacterial response to hydration and dehydration in a desert biological soil crust. *The ISME Journal*, *7*, 2178–2191.

Rasmussen, B., Fletcher, I. R., Brocks, J. J., & Kilburn, M. R. (2008). Reassessing the first appearance of eukaryotes and cyanobacteria. *Nature*, *455*, 1101–1104.

Raymond, J., Zhaxybayeva, O., Gogarten, J. P., Gerdes, S. Y., & Blankenship, R. E. (2002). Whole-genome analysis of photosynthetic prokaryotes. *Science*, *298*, 1616–1620.

Schlesinger, W. H., & Bernhardt, E. S. (2013). *Biogeochemistry: An analysis of global change*, San Diego: Academic Press.

Sciuto, K., & Moro, I. (2015). Cyanobacteria: The bright and dark sides of a charming group. *Biodiversity and Conservation*, *24*, 711–738.

Soo, R. M. (2015). In search of non-photosynthetic Cyanobacteria.

Soo, R. M., Hemp, J., Parks, D. H., Fischer, W. W., & Hugenholtz, P. (2017). On the origins of oxygenic photosynthesis and aerobic respiration in Cyanobacteria. *Science*, *355*, 1436–1440.

Soo, R. M., Skennerton, C. T., Sekiguchi, Y., Imelfort, M., Paech, S. J., Dennis, P. G., … Hugenholtz, P. (2014). An expanded genomic representation of the phylum Cyanobacteria. *Genome Biology and Evolution*, *6*, 1031–1045.

Stal, L. J. (2012). Cyanobacterial mats and stromatolites. In B. A. Whitton (Ed.), *Ecology of Cyanobacteria II* (pp. 65–125). Dordrecht: Springer.

Stal, L. J., & Moezelaar, R. (1997). Fermentation in cyanobacteria. *FEMS Microbiology Reviews*, *21*, 179–211.

Taton, A., Grubisic, S., Balthasart, P., Hodgson, D. A., Laybourn-Parry, J., & Wilmotte, A. (2006). Biogeographical distribution and ecological ranges of benthic cyanobacteria in East Antarctic lakes. *FEMS Microbiology Ecology*, *57*, 272–289.

Thompson, L. R., Sanders, J. G., McDonald, D., Amir, A., Ladau, J., Locey, K. J., … Zhao, H. (2017). A communal catalogue reveals Earth's multiscale microbial diversity. *Nature*, *551*, 457–463.

Utami, Y. D., Kuwahara, H., Murakami, T., Morikawa, T., Sugaya, K., Kihara, K., … Hongoh, Y. (2018). Phylogenetic diversity and single-cell genome analysis of "*Melainabacteria*", a non-photosynthetic cyanobacterial group, in the termite gut. *Microbes and Environments*, *33*, 50–57.

Wang, W., Wang, Y., Shu, X., & Zhang, Q. (2013). Physiological responses of soil crust-forming cyanobacteria to diurnal temperature variation. *Journal of Basic Microbiology*, *53*, 72–80.

Warnecke, F., Luginbühl, P., Ivanova, N., Ghassemian, M., Richardson, T. H., Stege, J. T., … Leadbetter, J. R. (2007). Metagenomic and functional analysis of hindgut microbiota of a wood-feeding higher termite. *Nature*, *450*, 560–565.

Warren-Rhodes, K. A., Rhodes, K. L., Pointing, S. B., Ewing, S. A., Lacap, D. C., Gómez-Silva, B., … McKay, C. P. (2006). Hypolithic cyanobacteria, dry limit of photosynthesis, and microbial ecology in the hyperarid Atacama Desert. *Microbial Ecology*, *52*, 389–398.

Whitton, B. A., & Potts, M. (2012). Introduction to the cyanobacteria. In B. A. Whitton (Ed.), *Ecology of Cyanobacteria II* (pp. 1–13). Dordrecht: Springer.

Whitton, B. A., & Sinclair, C. (1975). Ecology of blue-green algae. *Science Progress*, *62*, 429–446.

Williams, L., Loewen-Schneider, K., Maier, S., & Büdel, B. (2016). Cyanobacterial diversity of western European biological soil crusts along a latitudinal gradient. *FEMS Microbiology Ecology*, *92*, fiw157.

Wrighton, K. C., Castelle, C. J., Wilkins, M. J., Hug, L. A., Sharon, I., Thomas, B. C., … Banfield, J. F. (2014). Metabolic interdependencies between phylogenetically novel fermenters and respiratory organisms in an unconfined aquifer. *The ISME Journal*, *8*, 1452–1463.

Yagi, J. M., Neuhauser, E. F., Ripp, J. A., Mauro, D. M., & Madsen, E. L. (2010). Subsurface ecosystem resilience: Long-term attenuation of subsurface contaminants supports a dynamic microbial community. *ISME Journal*, *4*, 131–143.

Zhang, Y. (2005). The microstructure and formation of biological soil crusts in their early developmental stage. *Chinese Science Bulletin*, *50*, 117–121.

Zomer, R. J., Trabucco, A., & Bossio, D. A. (2008). Climate change mitigation: A spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. *Agriculture, Ecosystems & Environment*, *126*, 67–80.

BIOSKETCH

Concha Cano-Díaz is a biologist interested in the distribution and ecological drivers of soil cyanobacteria. She is currently studying the effects of climate change and soil formation processes on cyanobacterial communities around the world.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Cano-Díaz C, Maestre FT, Eldridge DJ, et al. Contrasting environmental preferences of photosynthetic and non-photosynthetic soil cyanobacteria across the globe. *Global Ecol Biogeogr.* 2020;29:2025–2038. https://doi.org/10.1111/geb.13173