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Role of environmental drivers in phototrophic organisms thriving in the caves of America: a systematic review with quantitative synthesis

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Abstract

Caves are an ideal niche for photosynthetic microorganisms with the morphological and physiological adaptations to thrive under extreme conditions. Microclimatic conditions, mainly light, temperature, and relative humidity, vary depending on the location and configuration of these cavities. A systematic review with quantitative synthesis was conducted to identify which environmental and ecological factors favored the growth of algae and Cyanobacteriophyta in cave environments of the American continent. To this end, results of studies from 26 caves, corresponding to 10 countries of the American continent, were analyzed. The species number recorded was 358, of which Bacillariophyceae predominated, followed by Cyanobacteriophyta, Chlorophyta, Rhodophyta, Phaeophyceae, Dinoflagellata, and Glaucophyta. The Shannon index determined that the diversity derived from the compiled literature of algae and Cyanobacteriophyta that thrive in these environments was 4.94, which is remarkably high. Nitzschia and Navicula were the most diverse Bacillariophyceae genera, while Oscillatoria and Phormidium dominated among Cyanobacteriophyta, and for Chlorophyta, Chlorella and Scenedesmus were the most diverse. However, Rhodophyta, Phaeophyceae, Dinoflagellata, and Glaucophyta were less diverse. An exploratory principal component analysis suggests that algal and cyanobacterial thriving is determined more by humidity and cave type than by temperature and photosynthetically active radiation.

Keywords: Chasm, Cyanobacteria, Diatoms, Dinophyceae, Hole, Karst, Rock shelter.

Introduction

Caves vary in their length and depth from a few to several thousand meters (Ford & Williams, 2007; Palmer, 1991). They are formed by different geological processes, such as erosion caused by water, volcanic activity, or the dissolution of soluble rocks such as limestone (Klimchouk, 2012).

Caves can be classified according to multiple criteria established by different authors. For instance, Jayasingha (2010) classify them according to the following criteria: location on earth (surface and underground), rock type (limestone, gypsum, and lava caves), morphology (rock shelter, hollow cave, tunnel cave, river cave, boulder cave, and crevice), moment of formation (primary and secondary caves), formation process (karst caves, lava tunnels caves, sea caves, and talus caves), rock age, and ecological sensitivity. Lazaridis (2022), for his part, classifies caves according to the process of speleogenesis into construction caves (sedimentary, biogenic, and volcanic caves), destruction caves (erosion/weathering, and karst caves), and multi-process caves (composite caves and the overprinted caves).

On the other hand, Ford & Williams (2007) and De Waele & Gutierrez (2022) classify caves according to the mineral composition of the rock as follows: carbonate caves (calcite and dolomite), sulphate caves (magnesite, anhydrite, and gypsum), halogen caves (halite, carnallite, sylvite, and polyhalite), and silica caves (silica and opal).

The different types of cave classification systems shown allow for the development of different lines of research depending on the approach. However, none of these classifications is based on the availability of light, a very important aspect when working with autotrophic organisms.

Caves are usually humid environments with low levels of natural light and generally stable temperature and humidity (Culver & Pipan, 2019). Their geology, structure of the rocks, mineral composition, and levels of temperature, light, humidity, and pH, among other environmental factors, make each cave a different, unique ecosystem (Northup & Lavoie, 2001). These ecosystems favor the dwelling of species which, thanks to physiological and metabolic adaptations, can thrive under those environmental conditions (Azúa-Bustos et al., 2009; Kociolek et al., 2013; Sánchez et al., 2002).

According to Xiong et al. (2023), the variability of the microclimate in caves can be influenced by factors such as air movement, cave structure, and the physical conditions of the environment. This variability in environmental parameters influences the composition and density of communities of phototrophic microorganisms (De Luca et al., 2021; Fernández & Salemme, 2012; Scheffler et al., 2019).

Despite the low availability of nutrients, caves provide an ecological niche for a wide spectrum of microorganisms (Barton & Northup, 2007). Most of these microorganisms reach caves through infiltration water, air currents, sediment displacement, and animal transport (Kuzmina et al., 2012). Secondary colonization of caves depends on the environmental conditions and the bioreceptivity of the different substrates (Griffin et al., 2014; Miller et al., 2009).

According to Hoffmann (2002), based on their degree of dependence on surviving in underground environments, the species that inhabit caves can be classified as troglobiotic (unable to survive outside caves), troglophilic (although they can live elsewhere, show a preference for cave-dwelling conditions), and trogloxenic (use caves occasionally without being adapted to them). The studies on cave microbiota began in the nineteenth century. So far, a wide spectrum of microorganisms capable of colonizing these cavities has been reported, including prokaryotes and eukaryotes (e.g., fungi, yeasts, algae, etc.) (Ghosh et al., 2017; Raji et al., 2019). Microbiological diversity studies, using culture-dependent and non-culture-dependent techniques, have shown that there is high bacterial diversity in caves. Among the bacterial taxa most frequently observed in caves are, from the most frequent to the least frequent, Proteobacteria (Alphaproteobacteria, Gammaproteobacteria, Betaproteobacteria), Acidobacteria, Firmicute Planctomycetes, and Actinobacteria (Barton & Jurado 2007; Zhou et al., 2007). As for fungi, the most frequently reported genera are, from the most frequent to the least frequent, Histoplasma Darling, Aspergillus Michelli, Penicillium Link, Fusarium Link ex Grey, among others (Vanderwolf et al., 2013). In relation to phototropic organisms, algae and Cyanobacteriophyta are the most frequently found in caves (Albertano, 2012).

In natural spaces, most microorganisms grow by forming communities attached to surfaces that are called biofilms, which favors their survival in harsh environments (Villa & Cappitelli, 2019). In caves, photosynthetic biofilms are found on the rocky substrate (epilithic), in pores and cavities (cryptoendolithic), in crevices (casmoendolithic), and under translucent surfaces (euendolithic) (Golubic et al., 1981). Microbial growth can be involved in destructive processes to the substrate, causing biodeterioration. This can be defined as any unwanted change in the properties of a material caused by the vital activities of an organism, and which can lead to partial or total disintegration of substrate or pigments in cave paintings (Di Carlo et al., 2022; Gaylarde et al., 2012).

In caves with rock art, biological colonization is one of the major problems due to the relationship between microbial colonization and biodeterioration, affecting the conservation of paints and causing serious aesthetic problems. The first research team to demonstrate the relationship between the formation of biofilms and the deterioration in rock art was Lefèvre et al. (1969) in the Lascaux Cave in France. Many similar results have been found elsewhere, e.g., in the Cave of the Holy Savior Vallerano, Italy (Zucconi et al., 2012), the Sistema Ventania Hill, Buenos Aires, Argentina (Guiamet et al., 2008), and the Caves of Murcia, Spain (Asencio & Aboal, 2000).

Cave dwelling microorganisms, especially Cyanobacteriophyta, have different functions, such as the formation and dissolution of rocks and minerals (Ehrlich, 1996; Cañaveras et al., 2001; Jones & Northup, 2021), and formation of speleothems such as stalactites and stalagmites (Davis & Rands, 1982; Harshberger, 1914; Zhu et al., 2022). These organisms also stand out as primary producers and synthesizers of secondary metabolites with biotechnological potential: antibiotics, siderophores, pigments, and enzymes (Candiroglu & Gungor, 2017). The study of these microorganisms in underground environments can also be an important model for understanding evolution and species diversity since Cyanobacteriophyta display ancestral features thought to be present during the early stages of the evolution of oxygenic photosynthesis, a process that led to the accumulation of oxygen in the Earth's atmosphere. These studies help to fill the gap in how oxygenic cyanobacteria first arose and diversified on the early Earth (Asencio & Aboal, 1996a, Kilgore et al., 2018; Saw et al., 2021).

As noted above, Cyanobacteriophyta and algae are the photosynthetic organisms most found in caves (Albertano, 2012). These organisms often colonize the entrance to the cave because natural lighting favors their growth (MacCaughey, 1918). However, in touristic caves, due to the use of artificial light, they colonize all the spaces impacted by light (Burgoyne et al., 2021; Smith & Olson, 2007). The group of phototrophic organisms dwelling around artificial lights is called lampenflora (Mulec & Kosi, 2009). The term lampenflora (German for "lamp flora" or "flora of the lamps") was coined by the German botanist Klaus Dobat (1963). The lampenflora mainly comprises three types of microscopic phototrophs: Cyanobacteriophyta, green algae, and diatoms. Cyanobacteriophyta are usually pioneer organisms in harsh environments. In the lampenflora, however, the first colonizers are commonly fast-growing green algae that are then covered by Cyanobacteriophyta (Mulec, 2019).

At the beginning of the twentieth century, the first references appear in literature about the presence of chlorophyll-containing organisms in caves, especially algae, as for example in the writings of Maheau (1903) and Lemmermayer (1912-1916). Since then, numerous studies have confirmed the presence of Cyanobacteriophyta and algae in cave systems worldwide, which confirms the importance of studying the role of these organisms in underground ecosystems.

The objective of this article is to analyze the results of research on Cyanobacteriophyta and algae communities in the American continent caves to identify which environmental and ecological factors favor the growth of these phototrophic organisms in those habitats.

Materials and Methods

Literature review

For this research, the literature on algal flora found in caves of all American countries was reviewed. Works that study Cyanobacteriophyta and algae in cave ecosystems of the American continent were selected, especially those that address issues such as biodiversity, ecology, and new species description. Studies that were located outside the geographical area of interest and those studies that did not explicitly mention the species of algae and Cyanobacteriophyta found were excluded.

The bibliographic review was conducted in 2024. The scientific literature search included PubMed, Google Scholar, and EBSCOhost databases. Advanced searches were performed in these databases using Boolean operators (AND, OR, NOT) to refine the results:

Pubmed - the following search equations were used:

- ((Algae) AND (cave)) AND (America)
- ((Bacillariophyceae) AND (cave)) AND (America)
- ((Bacillariophyta) AND (cave)) AND (America)
- ((Diatom) AND (cave)) AND (America)
- ((Chlorophyceae) AND (cave)) AND (America)
- ((Chlorophyta) AND (cave)) AND (America)
- ((Green algae) AND (cave)) AND (America)
- ((Cyanobacteria) AND (cave)) AND (America)
- ((Cyanophyceae) AND (cave)) AND (America)
- ((Cyanophyta) AND (cave)) AND (America)
- ((Cyanoprokaryota) AND (cave)) AND (America)
- ((Rhodophyceae) AND (cave)) AND (America)

- ((Rhodophyta) AND (cave)) AND (America)
- ((Red algae) AND (cave)) AND (America)

Google scholar - the following search equations were used:

- Bacillariophyceae AND cave AND America
- Bacillariophyta AND cave AND America
- Diatoms AND cave AND America
- Chlorophyceae AND cave AND America
- Chlorophyta AND cave AND America
- Green algae AND cave AND America
- Cyanobacteria AND cave AND America
- Cyanophyceae AND cave AND America
- Cyanophyta AND cave AND America
- Cyanoprokaryota AND cave AND America
- Rhodophyceae AND cave AND America
- Rhodophyta AND cave AND America
- Red algae AND cave AND (America)

EBSCOhost: -we performed an advanced search by placing key terms related to our research, we apply the filter of geographic location, academic publications, Spanish, and English language. To perform the most efficient search, we used the Boolean markers AND and OR, and we also used keyword filters in title and geography delimitation.

- TI Diatoms OR TI Bacillariophyta OR TI Bacillariophyceae AND TI cave AND TI America
- TI Chlorophyceae OR TI Chlorophyta OR TI Green algae AND cave AND America
- TI Cyanoprokaryota OR TI Cyanophyta OR TI Cyanobacteria OR TI Cyanophyceae AND cave AND America
- TI Red algae OR TI Rhodophyceae OT TI Rhodophyta AND Cave AND America

A total of 99 articles were retrieved from the three databases; however, 69 of these were excluded because they were not directly related to the research topic, were duplicate records, or did not fall within the geographical area of interest. Thus, a total of 30 articles was considered in this study (Figure 1).

AlgaeBase (https://www.algaebase.org/), a Global Database that provides detailed information on the taxonomy, nomenclature, and habitat type (terrestrial, marine, or freshwater), was used to standardize the taxonomic information. The following books were also consulted to standardize taxonomy and concepts:

-Ecology of Cyanobacteria II. Their Diversity in Space and Time (2012), Whitton.

-Karst Hydrogeology, Geomorphology and Caves (2022), De Waele & Gutiérrez.

-Karst Hydrogeology and Geomorphology (2007), Ford & Williams.

A map was created using MapChart, an online tool for creating and adapting maps.

Statistical analysis

The analysis of the data obtained in this study was run with the help of Microsoft Excel 2016 and the statistical program STATA version 12.0 software (StataCorp LP., TX, USA). The Shannon Index (H') was calculated to determine the diversity of cave-dwelling algae and Cyanobacteriophyta species using the formula $H' = -\sum(pi\ ln(pi))$ where pi is the proportion of individuals of species i.

A principal component analysis (PCA) (with normalization) was performed to determine if there was any relationship between cave-dwelling algae and Cyanobacteriophyta species with environmental parameters recorded (temperature, relative humidity, and photosynthetically active radiation) and the types of caves (subterranean, marine, flooded, ice, and lava).

Results and Discussion

A total of 26 caves and shelters distributed in 10 countries of the American continent were analyzed (Figure 2). Most studies were found in the United States (13), followed by Chile (1), Brazil (2), Mexico (3), Venezuela (2), Argentina (1), Belize (1), Bermuda (1), Canada (1), and Colombia (1). Even though caves are ecosystems of great scientific interest, research on the biodiversity of algae and Cyanobacteriophyta in cave systems in the Americas is scarce. This reality contrasts with continents such as Europe, where the subject is being well researched; in Spain, Serbia, and Greece alone, the number of caves studied equals that of the entire American continent (Belda et al., 2023).

Types of caves

The reviewed studies show that there are various types of caves in the American continent (Figure 3). Of the 26 studied caves, 17 are underground caves (with or without lakes or waterfalls inside) that have species of Bacillariophyceae, Cyanobacteriophyta, Chlorophyta, Rhodophyta, Dinoflagellata, and Glaucophyta. The sea caves were five; they have Cyanobacteriophyta, Chlorophyta, and Phaeophyceae. The flooded caves were two (one with freshwater and another with brackish water); they have Bacillariophyceae, Cyanobacteriophyta, Chlorophyta, and Dinoflagellata. One ice cave was reported with Bacillariophyceae. One lava cave was found with Bacillariophyceae and Cyanobacteriophyta.

The predominance of underground caves over other types of caves could be because most geological processes and phenomena take place beneath the Earth's surface, and some of them have formed empty underground spaces in accordance with Garofano & Govoni (2012).

Substrate Type

The substrate composition of the caves studied (Figure 4) indicates that limestone caves were found in the highest proportion (68%), which coincides with the research of Barton *et al.* (2014). Also, a study of seven caves in Montenegro showed that all of them were mainly made up of limestone and calcite, which are types of carbonate rocks common in karst regions (Kozlova *et al.*, 2019). In addition, we found that the limestone rocks house species of Bacillariophyceae, Cyanobacteriophyta, Chlorophyta, Rhodophyta, Phaeophyceae, Dinoflagellata, and Glaucophyta.

The second most frequent substrate is made of basaltic andesite (13%), and they sustain species of Cyanobacteriophyta, Chlorophyta, and Rhodophyta. Sandstone, dolomite, and orthoquartzite make 3% of the rocks, and they are the substrate for species of Bacillariophyceae, Cyanobacteriophyta, Chlorophyta and Rhodophyta.

These results show that phototrophic organisms are more adapted to live on limestone rocks, followed by basaltic andesite and, finally, on sandstone, dolomite and orthoquartzite. This indicate that the composition and mineral characteristics of the substrate are key factors for the colonization of algae and Cyanobacteriophyta in caves in accordance with Zhu *et al.* (2019). Hence, the importance of authors adding more detailed information about the substrate in their studies, since the papers consulted for 10% of the caves included in this study did not present data on the composition of the substrate.

Environmental Data

In caves, humidity and temperature can be relatively constant but not completely unchanged (Badino, 2018). To run this research, we used temperature, photosynthetically active radiation (P.A.R.), and relative humidity values provided in the selected articles. Thirty-five percent of the reviewed studies have the measurement of at least one of these environmental parameters.

All the caves studied presented high relative humidity values, ranging from 60 to 96%. The Onyx Cave in Missouri, USA, had the highest humidity levels (92-96%), followed by the Crystal Cave in Kentucky, USA (80-90%). The high relative humidity present in the caves in this study is consistent with those reported by Martinez & Asencio (2010) in Gelada Cave, Spain (Martínez & Asencio, 2010), Cennamo *et al.* (2012) in The Sybil's Cave, Italy, Popović *et al.* (2015) in Bozana Cave, Serbia, and Vinogradova *et al.* (2009) in Sefunim Cave, Israel, among others. Several studies on diatoms, such as those conducted in Oregon Cave and Timpanogos Cave, both in the USA, indicate that cave areas with higher moisture content have greater species diversity than in dry spaces (Clair *et al.*, 1981; Clair & Rushforth, 1976).

According to Czerwik-Marcinkowska *et al.* (2015), Cyanobacteriophyta and algae are better adapted to thrive in moist places. A redundancy analysis (RDA) with data taken in biofilms in Serbian caves concludes that relative humidity was the only physical parameter that showed statistical significance, indicating that it is likely to play a crucial role in the thriving of microbial communities in various locations (Popović *et al.*, 2017).

High relative humidity in caves provides an environment appropriate to algal growth because these organisms require this condition to perform essential metabolic processes such as photosynthesis and reproduction. However, in the southeast of Spain, algae and Cyanobacteriophyta thrive in caves with very low relative humidity, as is the case of L'Aigua cave in Alicante and Los Grajos Cave in Murcia, where the minimum humidity can be, respectively, 24.7% (Beltrán & Asencio, 2009) and 24.3% (Aboal *et al.*, 2003).

Regarding temperature, our results show a temperature inside the studied caves, with values ranging from 9°C in Onyx Cave in Missouri, USA, to 25°C in Crystal and Maya Blue Caves in Mexico. Although the temperature inside caves is usually stable all year round, this stability can be altered by factors such as cave morphology and location. Depending on the morphology of the cave, the connection between the surface and the subsoil can vary from zero connectivity, when it is completely isolated from surface influences to abundant connectivity if there are many connections to the surface. Temperatures in caves are usually close to the average annual temperature of the surface above the cave. In temperate regions, the outside air temperature in summer remains above the cave temperature, and the opposite occurs during winter. However, in the tropics in general, the surface temperature drops below the cave temperature during most nights (Gabriel & Northup, 2013).

In research run in the caves of the National Historical-Artistic Park of Gobustan, Azerbaijan, the temperature influence on the abundance of algal taxa was studied by Mazina *et al*. (2023). They noted that, when algal cultures were incubated at temperatures between 24 and 27 °C, the algae abundance was like that of the corresponding native community. On the other hand, when the incubation temperature was 12 °C, the abundance of algal taxa was lower. These findings suggest that thermal conditions can significantly influence the composition of algal communities and may also be a determining factor in the adaptation of biological communities to the specific conditions of the caves in Gobustan.

Photosynthetically active radiation (P.A.R.) range from the compiled studies falls between 0.01 and 95 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Generally, values lower than 0.03 $\mu mol \cdot m^{-2} \cdot s^{-1}$ are very low for algae and Cyanobacteriophyta growth. However, several studies have reported species adapted to these limited light conditions, e.g., in Onyx Cave, Missouri, USA. *Physolinum* Printz and other organisms present have evolved specific adaptations to survive in extremely low light conditions (Davis *et al.*, 1989). In Gelada Cave, Spain, *Symphyonema cavernicolum* Asencio, Aboal and Hoffmann thrives in very low light conditions, suggesting that it grows optimally in low light (Martínez & Asencio, 2010). The growth of *Cyanidium* Geitler inside the Atacama Cave, Chile, with P.A.R. of 1 $\mu mol \cdot m^{-2} \cdot s^{-1}$, suggests that this species has adapted to low light environments since the areas where it develops have extremely low light intensities (Azúa-Bustos & Vicuña, 2010). On the other hand, Azua-Bustos *et al.* (2010) reported colonies of *Dunaliella* in cobwebs of caves from the Atacama Desert, where light is significantly unavailable. This indicates that this alga is adapted to limited light conditions, which is vital for its survival in the sub-area habitat, as this genus is often associated with aquatic environments.

Other studies have shown that there is a direct relationship between P.A.R. and algae and Cyanobacteriophyta growth. Behrendt Lars *et al.* (2020) indicate that in caves, there is a marked niche differentiation based on the level of light available in the habitat. Low light availability is a limiting factor for the growth and distribution of epilithic algae in coastal caves (Dayner & Johansen, 1991; Mayer *et al.*, 2016).

Several studies show that the density of algae and Cyanobacteriophyta in sites with less light intensity is lower than in places with higher light intensity, demonstrating that light is an essential factor, especially for algae growth in cave environments (Jones, 1965; Mulec & Kosi, 2008). Sites with higher light intensity show increased biofilm growth, suggesting that light is a crucial factor for the growth of Cyanobacteriophyta and algae (Havlena *et al.*, 2021). Also, in the cave of La Serreta, the growth of algae and Cyanobacteriophyta is closely related to P.A.R. (Asencio & Aboal, 1996b). According to the study, algae and Cyanobacteriophyta showed optimal thriving under higher P.A.R. conditions, suggesting that the availability of light is a crucial factor for their development, specifically for caves (Asencio & Aboal, 1996b). In addition, in La Serreta Cave, the development of *Symphyonema cavernicolum* was epilithic in the areas of the cave less illuminated, while it was casmoendolithic in the sites with greater illumination. According to the authors, this behavior may be related to strategies of protection at high intensities of light (Asencio & Aboal, 1996b).

Although P.A.R. is an important determinant, its effect on algae growth depends on other environmental factors, such as temperature and relative humidity (Asencio & Aboal, 2000). According to Pentecost & Whitton (2002), caves are an excellent natural laboratory for investigating changes in lighting under near-constant temperature conditions.

Phototrophic microorganisms in the caves

In the 30 articles reviewed, 358 species of algae and Cyanobacteriophyta were found to dwell in 26 caves of the Americas. The group with more species is Bacillariophyceae with 212 species, followed by Cyanobacteriophyta with 94 species, Chlorophyta with 49 species, Rhodophyta with five species, Phaeophyceae with four species, Dinoflagellata with two species, and Glaucophyta with one specie.

Shannon index (H') was 4.94, indicating that the diversity of the phototrophic microorganism's species developing in the studied caves, derived from the compiled literature, is remarkably high. This is higher than H' estimated by Gainutdinov *et al.* (2017) for six caves in the Ural Bashkirskiyi Biosphere Reserve (Republic of Bashkortostan), where H' was 4.05. Therefore, caves and rock shelters represent centers of biodiversity for different types of microorganisms, particularly Bacillariophyceae and Cyanobacteriophyta, which can be widespread inhabitants on cave rock surfaces. The present study confirms this because, of all the works analyzed, the dominant group of phototrophic microorganisms in terms of number of species is Bacillariophyceae (Table 1). In consequence, cave environments can be considered understudied environments in terms of biodiversity, according to Asencio & Espinosa (2013).

Algae diversity

Algae were the most frequent phototrophic microorganisms in the caves studied. The total number of algae was 264 (Table 1), and their presence varies from one cave to another. In the Tsi-it-toh-Choh and Bear Canada ice caves, the largest number of algae reported was 97 species (Lauriol *et al.*, 2006), followed by Devil Hole in the U.S., where 54 species of algae were found (Shepard *et al.*, 2000). Meanwhile, caves with the lowest number of algae include Crystal Cave, USA with five species (Nagy, 1965), The Peñon Cave, Colombia (Pineda & Lasso, 2019), Charles Brewer Cave (Lundberg *et al.*, 2010), and Roraima Sur Cave (Barton *et al.*, 2014), both in Venezuela, with three species each, and Hawaiian Cave (MacCaughey, 1918) and Onyx Cave (Davis *et al.*, 1989), both in the USA, with two species.

In this research, the most frequently found algae groups (Figure 5) were Bacillariophyceae (76.9%), followed by Chlorophyta (18.6%). In contrast, Rhodophyta, Phaeophyceae, Dinoflagellata, and Glaucophyta were found to be a lower proportion with 1.9%, 1.5%, 0.8%, and 0.4%, respectively. The results are consistent with those reported in Karlamanskaya Cave in Russia (Dubovik, 2024) and in caves in southern Africa (Van Vuuren *et al.*, 2019), where Bacillariophyceae was the most frequently reported group, followed by Chlorophyta. This may be due to more favorable conditions, with higher levels of light and humidity inside the cave. Several studies conclude that the Rhodophyta is one of the least frequent groups of algae found in caves (Belda *et al.*, 2023; Gogoleva *et al.*, 2024). It is often overlooked by ecologists and taxonomists due to its rarity and also to taxonomic difficulties and lack of suitable identification keys (Eloranta & Kwandrans, 2007)

The most common genera within Bacillariophyceae were *Nitzschia* Hassall (17 species), *Navicula* Bory (15 species), *Cymbella* C.Agardh (11 species), and *Achnanthes* Hassall (seven species). These results differ from those obtained in subterranean ecosystems by Falasco *et al.* (2014), in which the most frequent species were *Hantzschia amphioxys* (Ehrenberg) Grunow, *Diadesmis contenta* (Grunow) D.G.Mann, and *Aerophilia roeseana* (Rabenhorst) Danz, Van de Vijver & Kociolek. In relation to the Chlorophyta division, the most frequent genera were *Chlorella* Beyerinck [Beijerinck] (three species) and *Desmodesmus* (Chodat) S.S.An, T.Friedl & E.Hegewald and *Stigeoclonium* Kützing (both with two species). This finding coincides with a study of 25 caves in Polish Jura, Poland, in which *Chlorella vulgaris* Beijerinck was among the most abundant Chlorophyta species (Czerwik-Marcinkowska & Mrozińska, 2011).

The group Bacillariophyceae was found in subterranean, marine, lava, and flooded caves. Eleven species were found in three types of caves (underground, marine, and lava). All members of this group (203 in total) were found in limestone except *Achnanthidium* sp., which was found in sandstone, and *Eunotia* sp., which, in addition to limestone, was found in sandstone. They developed at a temperature of 9–25.5 ºC, the relative humidity ranged from 80–96%, and they grew over a wide P.A.R. range: 0.01–95 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Members of the group Bacillariophyceae are considered cosmopolitan organisms (Mora *et al.*, 2015).

On the other hand, the Chlorophyta division developed in subterranean, marine, and flooded caves, on limestone, andesite, and orthoquartzite substrates at a temperature between 9 and 25.5 ºC. *Monoraphidium minutum* (Nägeli) Komárková-Legnerová and *Spirogyra* sp. thrive in a very narrow temperature range from 22.5 to 25.5 ºC. The relative humidity at which the members of this division developed was 68–96%, while the P.A.R. values ranged from 0.01 to 12.9 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Chlorophyta is characterized by colonizing a wide variety of environments, both aquatic and terrestrial, so they have a wide range of ecological adaptations (Jana, 2024).

The Rhodophyta species were found in underground and marine caves, on limestone, andesite, and sandstone substrates. They dwell at a temperature of 14–18 ºC, relative humidity ranged from 60–90%, and limited P.A.R. of 1–3 $\mu mol \cdot m^{-2} \cdot s^{-1}$, according to their environmental requirements (Eloranta & Kwandrans, 2007). In the Charles Brewer sandstone cave in Venezuela, Rhodophyta was observed to be the crucial component of the photosynthetic community along with Bacillariophyceae, a difference to the majority of studied caves, due to the acidic nature of the substrate, which is generally less suitable for Cyanobacteriophyta (Hauer *et al.*, 2015).

All members of Phaeophyceae were found in sea caves on limestone substrate. A discussion considering ecological aspects involving this division is limited, since none of the studies contained environmental data. These results are expected as this division is almost exclusively marine, with only a few exceptions that inhabit freshwater (Kumar & Singh, 1979; Gerovasileiou & Bianchi, 2021)

Dinoflagellata was found in underground, flooded caves, exclusively on limestone, for which the only environmental data found was the temperature, which remained constant between 25.2–25.5 °C. Although the members of this group are generally aquatic organisms in both marine and freshwater environments (Taylor *et al.*, 2008), Starmach (1963) already found dinoflagellates growing interspersed with cyanobacteria on the damp walls of the Twardowski cave in Kraków, Poland.

Cyanobacteriophyta diversity

The total number of Cyanobacteriophyta species present in the studied caves was 94 (Table 1), which ranked second in species number, after Bacillariophyceae (203). This result is in line with Hajong *et al.* (2021), who reported 95 species of algae from seven caves located in Meghalaya, India. In that study, the most representative group was Bacillariophyceae, followed by Cyanobacteriophyta and Chlorophyta. However, it contrasts with the work of Czerwik-Marcinkowska *et al*. (2015), carried out in caves in Ojców National Park, Poland, in which 62% of the taxa identified corresponded to Cyanobacteriophyta. It also differs from the meta-analysis conducted by Belda *et al.* (2023), in which Cyanobacteriophyta were the largest group of algae reported in caves around the world.

The 94 Cyanobacteriophyta species reported belong to the orders Oscillatoriales (29), Chroococcales (21), Nostocales (19), Gomontiellales (5) Synechococcales (5), Leptolyngbyales (4), Nodosilineales (3) Gloeobacterales (3), and Spirulinales (2). The least frequent orders were Acaryochloridales (1), Chroococcidiopsidales (1)

Choelofasciculales (1), and Stigonematales (1), grouped as other in Figure 6. The study conducted in limestone caves in Europe reports that the most abundant order of Cyanobacteriophyta was Chroococcales, represented by eight genera, while the least abundant was Nostocales with only three genera (Czerwik-Marcinkowska & Massalski, 2018).

The Cyanobacteriophyta genera with more species were *Oscillatoria* Vaucher ex Gomont (12 species), *Phormidium* Kützing ex Gomont (seven species), followed by *Chroococcus* Nägeli*, Lyngbya* C.Agardh ex Gomont*,* and *Nostoc* Vaucher ex Bornet & Flahault (five species each). Our results are consistent with those of the study conducted at Otap Head Cave in Abkhazia, where the most prevalent Cyanobacteriophyta genera were *Chroococcus, Gloeocapsa* Kützing*, Oscillatoria,* and *Phormidium* (Popkova & Mazina, 2019). In addition, Van Vuuren *et al.* (2019) conclude that the most prevalent Cyanobacteriophyta in Skilpad Cave and Bushmen Cave, Africa, were *Phormidium, Oscillatoria,* and *Nostoc.* The fact that these genera are common in these caves indicates that they are well adapted to cave environments, probably thanks to the sheath that acts as a water reservoir.

According to our results, the order Oscillatoriales thrives in a greater temperature (9.5–25 °C) and P.A.R. (0.1 - 78 $\mu mol \cdot m^{-2} \cdot s^{-1}$) ranges, and high relative humidity content characteristic of all the caves in the study. In contrast, Chroococcales and Leptolyngbyales thrive at more limited P.A.R. and temperature ranges, 0.01–0.05 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and 9–14 °C. In Božana Cave (Serbia), it was found that the coccoid forms of Cyanobacteriophyta were abundant in sites with low light intensity (Popović *et al.*, 2015). According to Mulec *et al.* (2008), coccoid forms of Cyanobacteriophyta tolerate lower irradiance than other forms, so they can develop in environments with low light intensity more easily than other morphologies.

The orders Nostocales, Oscillatoriales, and Gloeobacterales were found in three types of caves. The first two are in underground, marine, and flooded caves, while the third is in underground, marine, and lava caves, even though it only had three species. The order Chroococcales was only found in underground and sea caves. Caves are considered centers of biodiversity for almost all groups of Cyanobacteriophyta. It has been observed that the biodiversity reported in natural rocks is much greater than in anthropogenic substrates (Hauer *et al.*, 2015).

According to our results, the orders Nostocales, Oscillatoriales, Chroococales, and Gloeobacterales colonize three types of substrates. The first three were found on limestone, andesite, and orthoquartzite, while the fourth was found on limestone, andesite, and dolomite. Carbonate substrates allow the colonization by a greater number of taxa of Cyanobacteriophyta and other microorganisms because the chemical and physical characteristics of carbonate rocks provide a more favorable environment for their thriving (Hauer *et al.*, 2015).

The species *Chroococcus turgidus* (Kützing) Nägeli*, Hapalosiphon intricatus* West & G.S.West, and *Synechococcus* sp. developed under limited P.A.R. conditions from 0 to 0.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$. However, *Acaryochloris* sp. and *Chroococcidiopsis* sp. were found in a wider range of 0 to 95 $\mu mol \cdot m^{-2} \cdot s^{-1}$. *Nostoc* sp. was found in underground caves colonizing limestone, andesite, and orthoquartzite, being the species found in most types of substrates. Some species of the genus *Nostoc*, such as *N. commune* Vaucher ex Bornet & Flahault, are especially prevalent in karst regions, particularly in areas with an abundance of limestone rock (Potts *et al.*, 2002).

According to the PCA (Figure 7), the first three axes explain 100% of the total variance (PC1, PC2, and PC3 with 37.09%, 31.61%, and 31.30%, respectively). These axes are linear functions of the species of algae and Cyanobacteriophyta that develop in the caves, of the environmental parameters recorded, and of the types of caves. Despite considerable overlapping, species tend to be located along the first axis, which seems to capture the humidity (H) and cave-type gradients. The second axis is associated mainly with temperature (T) and P.A.R. The exploratory PCA suggests that H and cave type conditions the development of algae and Cyanobacteriophyta species in caves more actively than T and P.A.R. These results coincide with Popovic *et al.* (2017), who pointed to relative humidity as the only physical parameter that showed statistical significance in a cave in Serbia, indicating a key role in the development of microbial communities.

Limitations of the Study, Future Research Perspectives, and Practical Recommendations

Although this study provides valuable information on the diversity of algae and cyanobacteria in cave environments across the American continent, as well as on the environmental and ecological factors that promote their growth, certain methodological limitations must be taken into account. Firstly, the data collected originate from studies with different objectives and sampling methods, which results in heterogeneity across the studies. Secondly, the application of different taxonomic criteria and identification methods, as well as microclimatic measurements obtained under non-standardized conditions, leads to a lack of taxonomic and ecological standardization across the sources. Addressing these limitations in future research would strengthen the generalizability of the results.

Future studies could expand on the current findings by researching photosynthetic organisms in caves and rock shelters throughout the American continent, since there are countries with a remarkable wealth of cave environments, often with enormous natural and cultural interest both nationally and internationally, for which we found no data on the diversity and ecology of algae and Cyanobacteriophyta in underground habitats. That was the case for Bolivia, Costa Rica, Dominican Republic, Ecuador, El Salvador, French Guyana, Guatemala, Guyana, Nicaragua, Panama, Paraguay, Peru, Suriname, and Uruguay, as well as the Caribbean islands.

In summary, our results demonstrate that microclimatic conditions largely determine the composition, distribution, and structure of the algal and Cyanobacteriophyta flora in caves, as suggested by the exploratory PCA, species are more selected by humidity and cave type conditions than temperature and P.A.R. These findings not only address the objectives out-lined at the beginning of the study but also provide a solid foundation for practical applications in the conservation and management of cave environments, as well as guidance for future research on the biodiversity of algae and Cyanobacteriophyta in cave systems in the Americas where is scarce and is a topic that still requires more research to expand knowledge.

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Authors' Contributions

Conceptualization: C. F-C, A. D. A. **Data curation**: C. F-C, M. R-D. **Formal analysis**: C. F-C, M. R-D., A.D.A. **Funding acquisition**: J. D. H-M, A. D. A. **Investigation**: C. F-C. **Methodology**: C. F-C., J. D. H-M., A. D. A. **Project administration**: A. D. A, J. D. H-M. **Resources Software:** J. D. H-M., M. R-D. **Software**: J. D. H-M, M. R-D. **Supervision**: A. D. A., J. H-M. **Validation**: C. F-C., A. D. A. **Visualization**: C. F-C., **Writing – review & editing:** C. F-C, J. H-M, A. D. A.

Conflict of Interest

The authors declare that they have no conflict of interest that could have influenced the report presented in this article.

Data Availability Statement

Datasets related to this article will be available upon request to the corresponding author.

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Table and Figure Captions

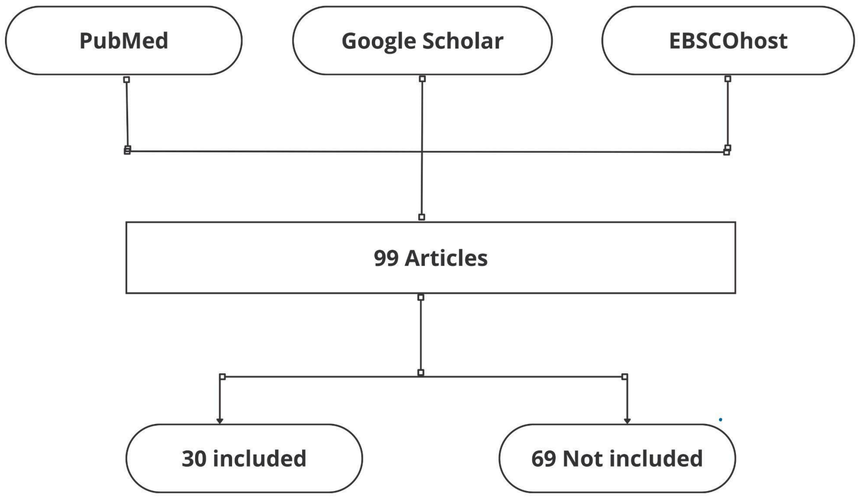

Figure 1. Search process for scientific articles in the different databases.

Figure 2. Geographical distribution of the caves included in this research, indicating the number of caves per country in parentheses.

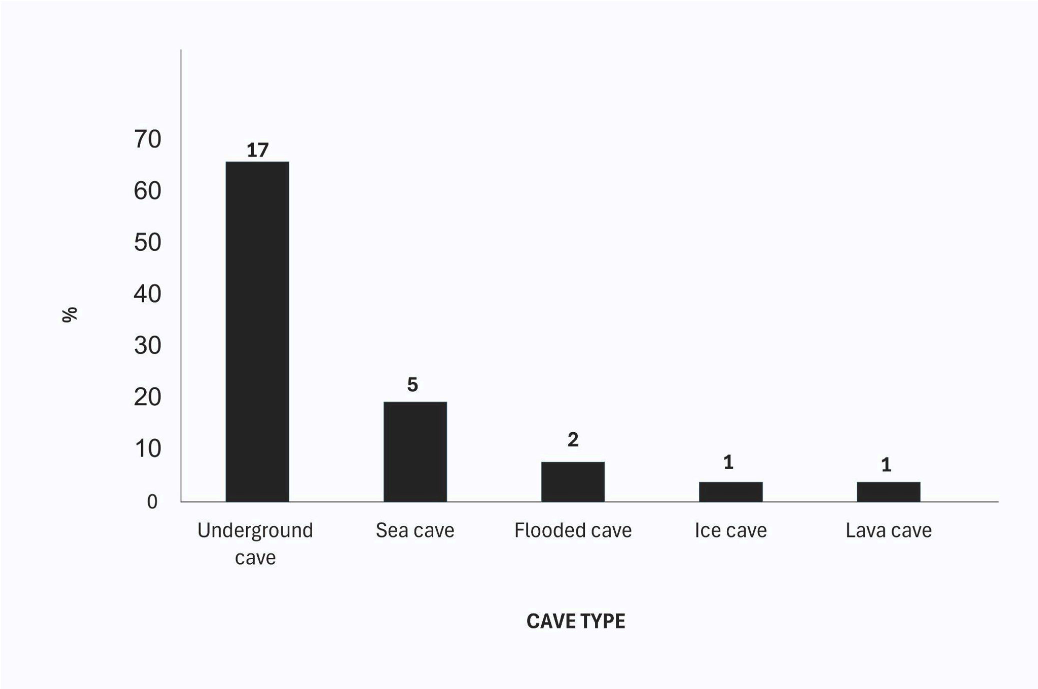

Figure 3. Number and percentage of cave types studied in the American continent.

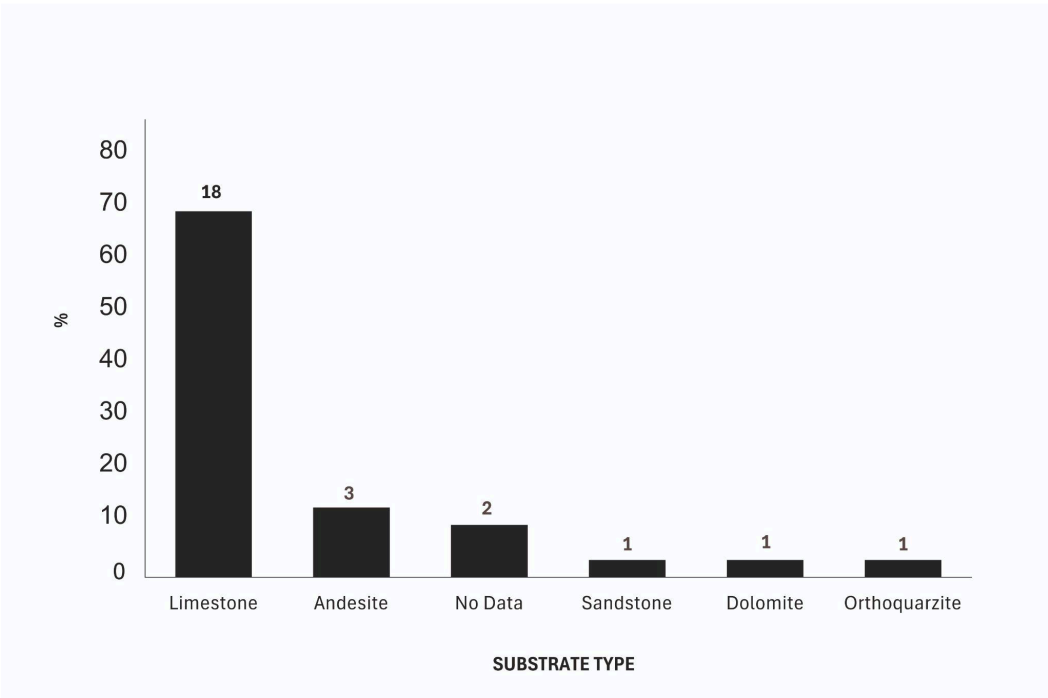

Figure 4. Number and percentage of the studied caves in the American continent according to the mineralogical composition of their substrate.

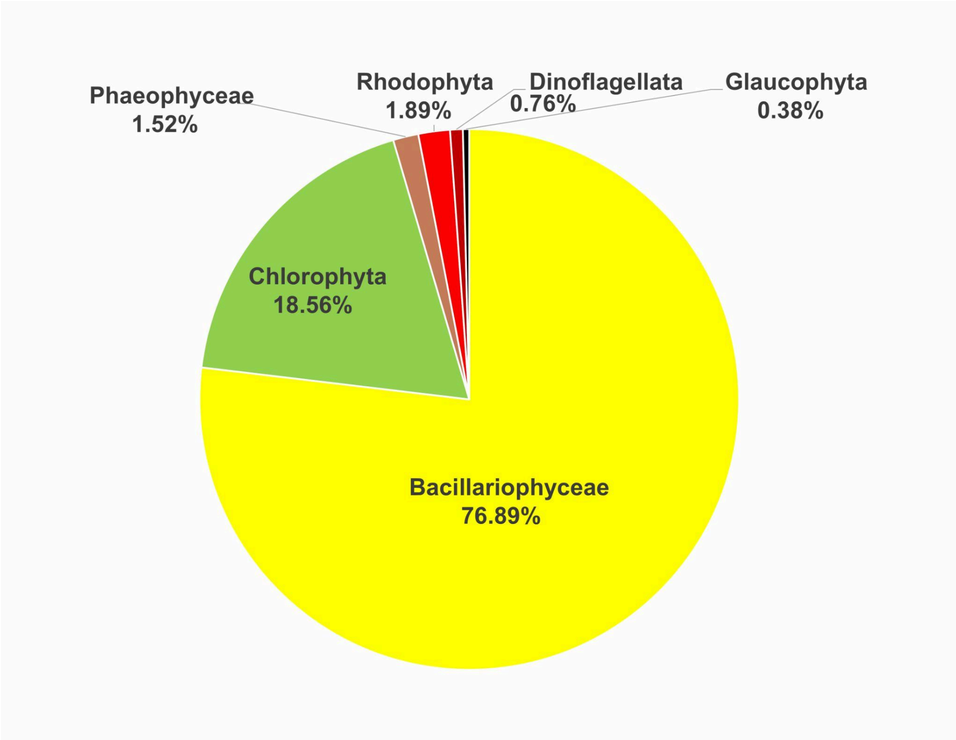

Figure 5. Distribution of algal groups found in the different caves studied in the American continent.

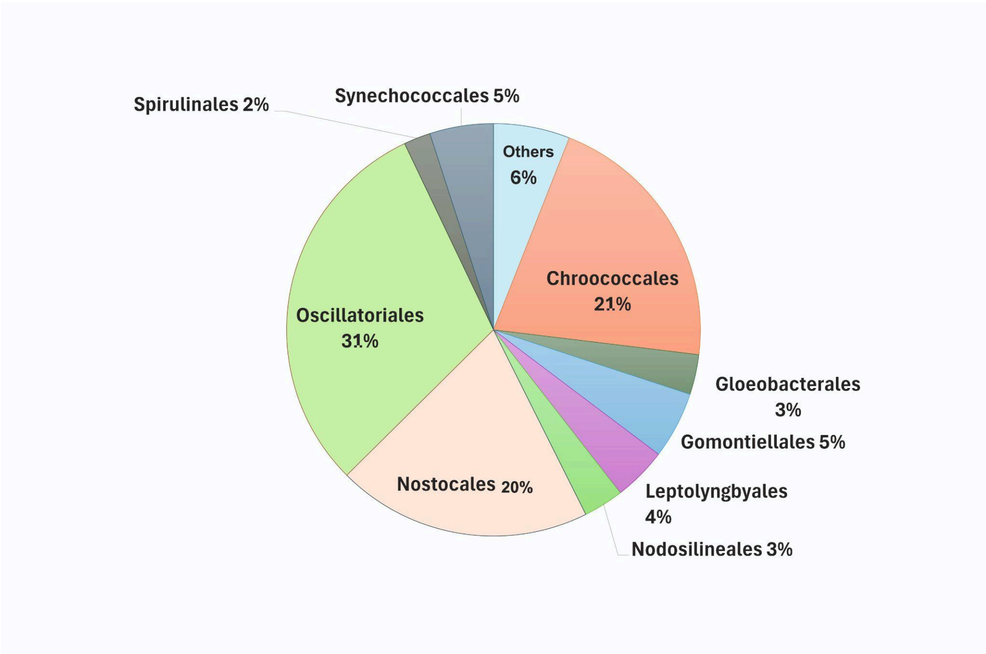

Figure 6. Distribution by Cyanobacteriophyta order found in the studied caves in the American continent.

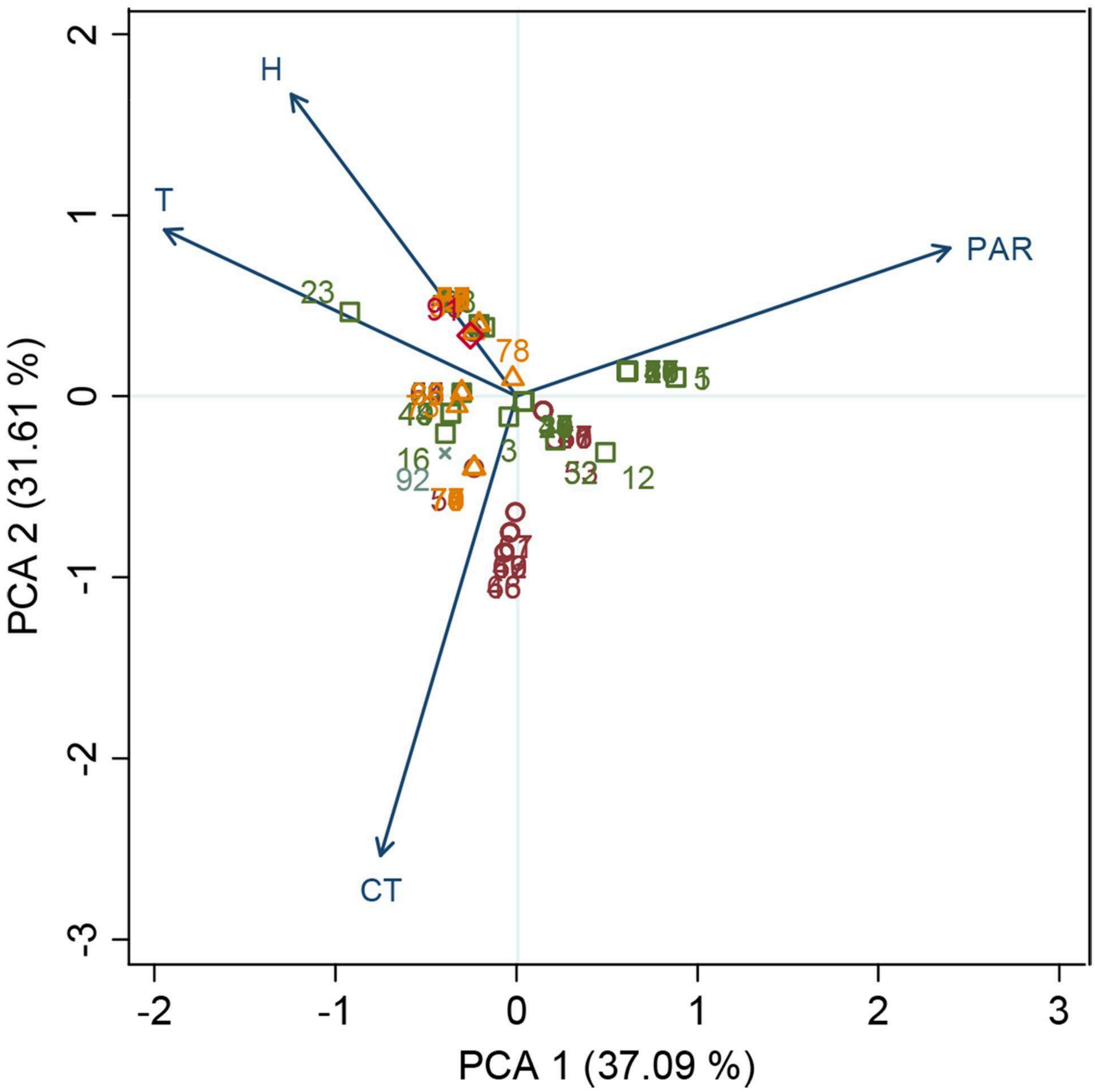

Figure 7. Principal component analysis (PCA) (with standardization) of 358 phototrophic species and microclimate conditions in cave environments as temperature in °C (T), % relative humidity (H), and photosynthetically active radiation in μmol·m^{-2}·s^{-1}, (P.A.R.), by cave type. Phototrophic species included (green open squares), Chlorophyta (orange open triangles), Bacillariophyceae (brown open circles), Rhodophyta (red open diamonds), Dinoflagellata (blue X), and Glaucophyta (black open circles).

	Temperature (°C)		Relative Humidity (%)		P.A.R. (µmol·m^{-2}·s^{-1})		Cave type	Substrate type	Argentina	Belize	Bermuda	Brazil		Canada	Chile	Colombia	United States													Mexico			Venezuela	
	Min	Max	Min	Max	Min	Max			Maripe Cave	Submarine cave near Columbus Cay	The Devil Hole	Bonito Cave	Laguna Misteriosa	Grand Cavern	The Atacama Cave	The Peñon Cave	Carlsbad Cavern	Caves close to Cades Cove y White Oak Sink	Crystal Cave	Devils Hole	Hawaiian Caves	Haena Cave	Kīlauea Caldera	Mammoth Cave	Onyx Cave	Orange Lake Cave	Oregon Cave	Seneca Cave	Timpanogos Caves	Crystal Cave	Maya Blue Cave	Waterfall cave	Charles Brewer Cave	Roraima Sur Cave
Cyanobacteriophyta																																		
Acaryochloris sp.					*0.04*	*95*	*A*	*1*									x																	
Anabaena sp.							*B*	*1*												x														
Anacystis montana var. *gelatinosa*							*B*	*1*												x														
Aphanocapsa muscicola	*15*				*77.67*		*A*	*1*																x										
Aphanocapsa sp.	*25.2*						*B*	*1*												x											x			
Aphanothece naegelii							*A*	*2*													x													
Aphanothece saxicola	*15*				*77.67*		*A*	*1*																x										
Calothrix thermalis							*B*	*1*												x														
Chamaesiphon sp.							*B*	*1*												x														

Chamaesiphon confervicola var. *angustus*							*A*	*1*											x															
Chlorogloeopsis sp.							*A*	*5*																										x
Chroococcidiopsis sp.					*0.04*	*95*	*A*	*1, 5*									x																	x
Chroococcus cohaerens	*15*				*77.67*		*A*	*1*																x										
Chroococcus helveticus	*15*				*77.67*		*A*	*1*																x										
Chroococcus minor	*15*				*77.67*		*A*	*1*																x										
Chroococcus sp.							*B*	*1*												x														
Chroococcus turgidus	*9*	*14*	*92*	*96*	*0.01*	*0.05*	*A, B*	*1*												x					x									
Cyanobacterium minervae							*B*	*1*												x														
Cyanothece aeruginosa	*15*				*77.67*		*A*	*1*																x										
Cyanothece sp.	*15*				*77.67*		*A*	*1*																x										
Fischerella ambigua							*A*	*2*													x													
Geitleria appalachiana							*A*	*1*										x																
Gloeobacter kilaueaensis							*D*	*2*															x											
Gloeobacter morelensis							*A*	*4*																								x		
Gloeobacter violaceus							*B*	*1*			x																							
Gloeocapsa sp.							*B*	*1*												x														
Gloeocapsa aeruginosa	*15*				*77.67*		*A, B*	*1*			x													x										
Gloeocapsa gelatinosa							*B*	*1*			x																							
Gloeocapsa quaternata							*A, B*	*1,2*			x										x													
Gloeotrichia echinulata	*13.8*	*17.5*	*80*	*90*	*1.3*	*12.9*	*A*	*1*									x																	
Gloeotrichia pisum	*13.8*	*17.5*	*80*	*90*	*1.3*	*12.9*	*A*	*1*									x																	
Gomontiella magyariana	*9.5*	*10.5*					*A*	*1*																x										

Hapalosiphon intricatus	*9*	*14*	*92*	*96*	*0.01*	*0.05*	*A, E*	*1*																	x	x								
Johannesbaptistia schizo dichotoma							*B*	*1*												x														
Leptolyngbya sp.	*13.8*	*17.5*	*80*	*90*	*1.3*	*12.9*	*A*	*1*									x																	
Leptolyngbya subtilissima	*15*				*77.67*		*A*	*1*																x										
Leptolyngbya tenuis	*15*				*77.67*		*A*	*1*																x										
Lyngbya limnetica							*B*	*1*												x														
Lyngbya majuscula							*B*	*1*												x														
Lyngbya pusilla	*9.5*	*10.5*					*A*	*1*																x										
Lyngbya truncicola	*15*				*77.67*		*A*	*1*																x										
Lyngbya sp.	*25.22*	*25.5*					*B*	*1*												x										x	x			
Merismopedia elegans							*B*	*1*																							x			
Microcoleus sp.							*A*	*5*																										x
Microcoleus vaginatus							*B*	*1*												x														
Microcystis flos-aquae							*B*	*1*			x																							
Microcystis stagnalis	*9.5*	*10.5*					*A*	*1*																x										
Microcystis sp.							*B*	*1*												x														
Myxosarcina amethystina							*B*	*1*												x														
Nodosilinea sp.	*13.8*	*17.5*	*80*	*90*	*1.3*	*12.9*	*A*	*1*									x																	
Nodosilinea foveolarum	*13.8*	*17.5*	*80*	*90*	*1.3*	*12.9*	*A*	*1*									x																	
Nodosilinea nodulosa	*13.8*	*17.5*	*80*	*90*	*1.3*	*12.9*	*A*	*1*									x																	
Nostoc minutissimum	*9.5*	*10.5*					*A*	*1*																x										
Nostoc muscorum	*15*				*77.67*		*A*	*1*																x				x						
Nostoc paludosum							*B*	*1*												x														

Nostoc punctiforme							*A*																				x						
Nostoc sp.	*9*	*17.5*	*80*	*96*	*0.01*	*12.9*	*A*	*1, 2, 5*								x				x				x			x						x
Oscillatoria amphibia							*B*	*1*											x														
Oscillatoria amphigranulata							*B*	*1*											x														
Oscillatoria animalis	*9.5*	*10.5*					*A*	*1*															x										
Oscillatoria clausiana	*9.5*	*10.5*					*A*	*1*															x										
Oscillatoria foreaui							*A*																				x						
Oscillatoria formosa							*A*	*2*												x													
Oscillatoria neglecta	*9.5*	*10.5*					*A*	*1*										x					x										
Oscillatoria princeps							*B*	*1*											x														
Oscillatoria rupicola	*15*				*77.67*		*A*	*1*															x										
Oscillatoria sancta							*A*	*2*												x													
Oscillatoria subtilissima	*9.5*	*10.5*					*A*	*1*															x										
Oscillatoria sp.							*B*	*1*											x														
Phormidium cebennense	*9.5*	*10.5*					*A*	*1*															x										
Phormidium papyraceum							*A*	*2*												x													
Phormidium priestleyi																			x														
Phormidium purpurascens							*B*	*1*											x														
Phormidium sp.	*13.8*	*17.5*	*80*	*90*	*1.3*	*12.9*	*A*	*1*								x																	
Phormidium subtruncatum	*9.5*	*10.5*					*A*	*1*															x										
Phormidium tenue							*B*	*1*																						x			
Planktothrix agardhii							*B*	*1*																						x			
Plectonema sp.							*B*	*1*											x														
Porphyrosiphon martensianus	*15*				*77.67*		*A*	*1*															x										

Raphidiopsis sp.							*B*	*1*												x														
Romeria gracilis	*13.8*	*17.5*	*80*	*90*	*1.3*	*12.9*	*A*	*1*									x																	
Scytonema sp.							*B, E*	*1*												x						x								
Scytonema julianum	*15*				*77.67*		*A*	*1*																x										
Scytonema ocellatum							*A*	*2*													x													
Scytonema varium							*A*	*2*													x													
Spirulina major							*A*	*2*													x													
Spirulina sp.							*B*	*1*																							x			
Symploca cartilaginea	*15*				*77.67*		*A*	*1*																x										
Symploca sp.	*13.8*	*17.5*	*80*	*90*	*1.3*	*12.9*	*A*	*1*									x																	
Synechocystis sp.	*9*	*14*	*92*	*96*	*0.01*	*0.05*	*A, B*	*1*												x					x									
Synechococcus lividus							*B*	*1*												x														
Synechococcus sp.	*9*	*14*	*92*	*96*	*0.01*	*0.05*	*A, B*	*1*												x					x									
Tetrachloris inconstans	*9.5*	*10.5*					*A*	*1*																x										
Thalpophila imperialis							*B*	*1*												x														
Trichormus variabilis							*A*	*2*													x													
Bacillariophyceae																																		
Achnanthes sp.							*B, C*	*1*	*X*					x						x														
Achnanthes brevipes							*B, C*	*1*																							x			
Achnanthes coarctata							*A*	*1*																			x		x					
Achnanthes exigua							*A, B*	*1*												x							x							
Achnanthes hauckiana							*B*	*1*																						x	x			
Achnanthes laevis							*C*	*1*						x																				
Achnanthes montana							*A*	*1*																			x							
Achnanthes petersenii							*C*	*1*						x																				
Achnanthes submarina							*B*	*1*												x														

Achnanthes suchlandtii							B	1												x														
Achnantheiopsis fragilarioides							C	1						x																				
Achnanthidium minutissimum	9.5						A, B, C	1						x						x				x			x				x			
Achnanthidium affine							B, C	1												x														
Achnanthidium biasolettianum							C	1						x																				
Achnanthidium lineare							A, B, C	1						x						x									x					
Achnanthidium sp.							A	3																									x	
Adlafia bryophila							C	1						x																				
Aerophilia roeseana							C	1						x																				
Anomoeoneis serians							B	1												x														
Amphora coffeaeformis							B	1																							x			
Amphora inariensis							C	1						x																				
Amphora lybica							C	1						x																				
Amphora pediculus							C	1						x																				
Amphora perpusilla							A	1																			x							
Amphora sp.							C	1						x						x														
Aulacoseira distans							A	1																					x					
Aulacoseira granulata							A	1																x										
Aulacoseira sp.	15	20					C	1						x																				
Brachysira aponina							B	1												x														
Brachysira vitrea							B, C	1						x																	x			
Bacillaria paradoxa							B	1																						x	x			
Caloneis bacillum							A	1																					x					
Caloneis silicula							B	1												x														
Caloneis sp.							B, C	1						x						x														
Caloneis ventricosa							B	1												x														
Chamaepinnularia begeri							C	1						x																				
Chlamydomyxa sp.	13.8	17.5	80	90	1.3	12.9	A	1									x																	
Cocconeis placentula							A, B, C	1						x										x					x		x			

Cocconeis sp.							B, C	1						x						x														
Coscinodiscus sp.							B, C	1												x														
Crenotia gibberula							B, C	1												x														
Cyclotella meneghiniana							B	1																							x			
Cyclotella sp.							B	1																						x				
Cymbella affinis							C	1						x																				
Cymbella aspera							C	1						x																				
Cymbella cesatii							B	1												x														
Cymbella cistula							C	1						x																				
Cymbella delicatula							A, B	1												x				x										
Cymbella fonticola							B	1												x														
Cymbella gracilis							B	1																							x			
Cymbella minuta							A, B, C	1						x						x							x							
Cymbella norvegica							B	1												x														
Cymbella silesiaca							C	1						x																				
Cymbella sp.	9.5						A, B, C	1						x		x				x				x										
Cymbopleura amphicephala							C	1						x																				
Cymbopleura angustata							B	1												x														
Denticula elegans							A, B	1	x											x														
Denticula sp.							A	1	x																									
Denticula tenuis														x																				
Denticula tenuis var. *crassula*							C	1						x																				
Diadesmis contenta var. *parallela*							C	1						x																				
Diadesmis sp.							C	1					x																					
Diatoma hyemalis							A, C	1						x															x					
Diatoma mesodon							C	1						x																				
Diatoma sp.	15	20					E	1					x																					
Diatoma vulgaris	9.5						A	1																x					x					
Didymosphenia geminata							C	1						x																				

Diploneis elliptica							*A*	*1*	x																									
Diploneis papula							*A*	*1*																			x							
Diploneis sp.							*C*	*1*						x																				
Diprora haenaensis							*A*															x												
Encyonema brehmii	*9.5*						*A*	*1*																x										
Encyonema latens							*C*	*1*						x																				
Encyonema leibleinii	*9.5*						*A*	*1*																x										
Encyonema muelleri							*B*	*1*																							x			
Encyonopsis descripta							*C*	*1*						x																				
Encyonopsis microcephala							*B, C*	*1*						x						x											x			
Entomoneis sp.							*B*	*1*																						x				
Eolimna minima							*A, B*	*1*												x							x							
Eolimna tantula							*A*																					x						
Eucocconeis flexella							*C*	*1*						x																				
Eunotia arcus							*B*	*1*												x														
Eunotia bidens							*C*	*1*						x																				
Eunotia minor							*B*	*1*																							x			
Eunotia monodon							*B*	*1*																							x			
Eunotia paludosa							*C*	*1*						x																				
Eunotia pectinalis							*B*	*1*												x														
Eunotia praerupta							*B, C*	*1*						x						x														
Eunotia sp.							*A, B, C*	*1, 3*						x		x				x													x	
Fallacia frustulum							*B*	*1*												x														
Fallacia insociabilis							*A*	*1*																			x							
Fistulifera pelliculosa							*A*	*1*																			x							
Fragilaria amphicephaloides							*B*	*1*																							x			
Fragilaria construens							*A*	*1*																			x		x					
Fragilaria rumpens	*9.5*						*A, B*	*1*												x				x										
Fragilaria sp.	*9.5*						*A, B, C*	*1*	x					x						x				x										

Fragilaria vaucheriae							B	1												x														
Gomphonema affine							B	1																						x				
Gomphonema angustatum							B, C	1						x						x														
Gomphonema angustatum var. *elongatum*							C	1						x																				
Gomphonema gracile							B	1																							x			
Gomphonema insigne	25.22	25.5					B	1																						x				
Gomphonema intricatum	25.22	25.5					B	1												x										x				
Gomphonema laetelanceolatum	9.5						A	1																x										
Gomphonema olivaceum							A	1																					x					
Gomphonema parvulum							B	1																							x			
Gomphonema productum							C	1						x																				
Gomphonema sp.	9.5						A, B, C	1						x						x				x										
Gyrosigma obscurum	25.22	25.5					B	1																						x	x			
Gyrosigma sp.							B	1																						x				
Hannaea arcus							B, C	1												x														
Hannaea arcus var. *amphioxys*							C	1						x																				
Hantzschia amphioxys							A, C	1						x													x		x					
Humidophila contenta							A, C	1						x										x										
Humidophila gallica							A, C	1						x													x							
Hygropetra balfouriana							C	1						x																				
Liparogyra dendrophila							C	1						x																				
Lemnicola hungarica							B	1												x														
Luticola goeppertiana							C							x																				
Luticola murrayi							A	1																					x					
Luticola mutica							C	1						x															x					
Luticola muticopsis							A, C	1						x					x															
Luticola nivalis							C	1						x																				

Luticola nivaloides							B, C	1						x						x														
Mastogloia smithii							B	1												x														
Mayamaea atomus							A	1																					x					
Mayamaea permitis							A	1																					x					
Melosira roseana	9	14	92	96	0.01	0.05	A	1																	x		x		x					
Melosira varians	9.5						A	1																x					x					
Meridion circulare	9.5						A, C	1						x										x										
Navicula amphibola							C	1						x																				
Navicula calcuttensis var. gracillis							C	1						x																				
Navicula contenta							A	1																					x					
Navicula cryptocephala							A, B, C	1						x															x		x			
Navicula cuspidata							C	1						x																				
Navicula digitoradiata	25.2	25.5					B	1																						x	x			
Navicula gracilis							C	1						x																				
Navicula minuscula							B	1																						x	x			
Navicula parva							B	1												x														
Navicula radiosa							A, B	1																					x	x	x			
Navicula rhynchocephala							C	1						x																				
Navicula semen							C	1						x																				
Navicula tripunctata							B	1												x														
Navicula sp.							B, C	1						x						x														
Neidium bergii							C	1						x																				
Neidium bisulcatum							C	1						x																				
Neidium sp.	25.22	25.5					B	1																						x				
Nitzschia sp.							A, B, C	1	x					x						x											x			
Nitzschia amphibia							B	1												x											x			
Nitzschia amphibioides	25.22	25.5					B	1																						x	x			

Nitzschia denticula							B	1												x														
Nitzschia dissipata							B	1												x														
Nitzschia fonticola							B, C	1						x						x														
Nitzschia frustulum							A, B	1												x									x		x			
Nitzschia hantzschiana							A, B	1												x				x										
Nitzschia kuetzingiana							B	1												x														
Nitzschia linearis							A	1																			x		x					
Nitzschia nana							C	1						x																				
Nitzschia palea							B	1												x														
Nitzschia paleacea							A, B	1												x							x							
Nitzschia perminuta							A	1																							x			
Nitzschia sigmoidea							B	1																							x			
Nitzschia vitrea							B	1												x														
Odontidium mesodon							A	1																					x					
Orthoseira dendroteres							C	1						x																				
Orthoseira sp.							C	1						x																				
Planothidium grimmei							B	1												x														
Planothidium lanceolatum							A, B	1												x									x					
Pinnularia biceps							C	1						x																				
Pinnularia borealis							A, C	1	x					x																				
Pinnularia brauniana							C	1						x																				
Pinnularia divergentissima							C	1						x																				
Pinnularia intermedia							A, C	1						x															x					
Pinnularia interrupta							A	1																					x					
Pinnularia microstauron							A	1	x																									
Pinnularia sp.	9.5						A,B, C	1						x		x				x				x										
Psammothidium kryophilum							C	1						x																				
Psammothidium marginulatum							C	1						x																				
Pseudoplanothidium delicatulum							B	1																							x			

Pseudostaurosira brevistriata							*A*	*1*	x																									
Rhopalodia sp.							*A*	*1*	x																									
Sellaphora secura							*A*	*1*																			x							
Surirella ovalis							*A*	*1*																					x					
Surirella sp.							*B*	*1*																						x				
Stauroneis agrestis							*C*	*1*						x																				
Stauroneis anceps							*C*	*1*						x																				
Stauroneis obtusa							*C*	*1*						x																				
Stauroneis phoenicenteron							*C*	*1*						x																				
Stauroneis sp.	*9.5*						*A C*	*1*																x										
Staurosira construens							*C*	*1*						x																				
Staurosira pseudoconstruens							*C*	*1*						x																				
Staurosirella pinnata							*A C*	*1*	x					x																				
Stephanodiscus astraea							*B*	*1*												x														
Stephanodiscus hantzschii							*A*	*1*																x										
Synedra sp.							*C*	*1*						x																				
Synedra ulna	*9.5*						*A, B, C*	*1*						x										x					x		x			
Tabellaria flocculosa							*B, C*	*1*						x						x														
Tabellaria sp.							*C*	*1*						x																				
Tabularia fasciculata							*B*	*1*																							x			
Terpsinoë musica							*B*	*1*																							x			
Tryblionella debilis							*C*	*1*						x																				
Tryblionella littoralis							*A*	*1*																x										
Ulnaria acus							*B*	*1*																							x			
Unidentified							*B*	*1*												x														
Chlorophyta																																		
Ankyra judayi	*13.8*	*17.5*	*80*	*90*	*1.3*	*12.9*	*A*	*1*									x																	
Ankistrodesmus falcatus							*A*	*1*																x										
Auxenochlorella protothecoides							*A*	*1*									x							x										

Characiopsis minuta							*A*	*2*													x													
Chlamydomonas sp.							*A*	*5*																										x
Chlorella miniata							*A*	*1*																x				x						
Chlorella sp.	*13.8*	*17.5*	*80*	*90*	*1.3*	*12.9*	*A, B*	*1,5*																						x				x
Chlorella vulgaris							*A, B*	*1*																x							x			
Chlorococcum sp.							*B*	*1*												x														
Closterium sp.	*15*	*20*					*E*	*1*						x																				
Coelastrum sp.	*15*	*20*					*E*	*1*						x																				
Crucigeniella sp.	*15*	*20*					*E*	*1*						x																				
Cylindrocystis brebissonii							*A*	*1*																x										
Desmidium sp.	*15*	*20*					*E*	*1*						x																				
Desmodesmus abundans							*A*	*1*																x										
Desmodesmus brasiliensis							*A*	*1*											x															
Dunaliella atacamensis	*18*		*68*		*1.4*		*A*	*2*								x																		
Ettlia minuta							*A, B*	*1*											x											x				
Euastrum sp.	*15*	*20*					*E*	*1*						x																				
Euastrum sublobatum							*A*	*1*																x										
Fusola viridis							*B*	*1*												x														
Gloeocystis vesiculosa							*A*	*1*																x										
Gloeocystis sp.							*B*	*1*												x														
Halimeda simulans							*B*			x																								
Iwanoffia terrestris							*A*	*1*																x										
Kirchneriella lunaris							*A*	*1*																x										
Klebsormidium flaccidum							*A*																					x						
Monoraphidium minutum	*25.22*	*25.5*					*B*	*1*																						x				
Neochloris sp.							*B*	*1*											x															
Netrium oblongum							*A*	*1*																x										
Oedocladium sp.							*B*	*1*												x														

Oocystis lacustris							*A*	*1*									X							X										
Prasiola crispa	*13.8*	*17.5*	*80*	*90*	*1.3*	*12.9*	*A*	*1*									X																	
Pedospumella sp.	*13.8*	*17.5*	*80*	*90*	*1.3*	*12.9*	*A*	*1*									X																	
Penicillus pyriformis							*B*			X																								
Picochlorum sp.	*13.8*	*17.5*	*80*	*90*	*1.3*	*12.9*	*A*	*1*									X																	
Physolinum sp.	*9*	*14*	*92*	*96*	*0.01*	*0.05*	*A*	*1*																	X									
Pseudochloris wilhelmii	*13.8*	*17.5*	*80*	*90*	*1.3*	*12.9*	*A*	*1*									X																	
Protococcus sp.							*A, B*	*1*												X														
Rhipocephalus phoenix							*B*			X																								
Scenedesmus sp.							*A, E*	*1, 5*					X																					X
Spirogyra sp.	*25.22*	*25.5*					*B*	*1*												X										X				
Stichococcus bacillaris	*13.8*	*17.5*	*80*	*90*	*1.3*	*12.9*	*A*	*1*									X																	
Stichococcus sp.	*13.8*	*17.5*	*80*	*90*	*1.3*	*12.9*	*A*	*1*									X																	
Stigeoclonium polymorphum							*A*																					X						
Stigeoclonium sp.							*B*	*1*																						X				
Treubaria triappendiculata	*13.8*	*17.5*	*80*	*90*	*1.3*	*12.9*	*A*	*1*									X																	
Udotea wilsonii							*B*			X																								
Ulothrix minutula							*A*	*2*													X													
Unidentified	*13.8*	*17.5*	*80*	*90*	*1.3*	*12.9*	*A*	*1*									X																	
Phaeophyceae																																		
Dictyota bartayresiana							*B*			X																								
Lobophora variegata							*B*			X																								
Padina sp.							*B*			X																								
Sargassum hystrix							*B*			X																								

Rhodophyta																																		
Audouinella sp.							A	3																									x	
Chroothece richteriana							B	1			x																							
Cyanidium sp.	14	18	60	90	1	3	A	1, 2				x			x																			
Paralemanea torulosa							A	1																x										
Unidentified							B	1			x																							
Dinoflagellata																																		
Borghiella tenuissima							A	1											x															
Peridinium sp.	25.22	25.5					E	1					x																					
Glaucophyta																																		
Glaucocystis nostochinearum							A	1									x																	

Table 1: Average environmental data (temperature (ºC), relative humidity (%), and photosynthetically active radiation (μmol·m^{-2}·s^{-1})) and phototrophic species collected in the different sites in the papers selected for this study. Authors of the cited algal and cyanobacterial taxa can be found in Algaebase (Guiry & Guiry, 2026). Cave type: A = Underground cave, B = Sea cave, C = Ice cave, D = Lava cave, E = Flooded cave. Substrate type: 1 = Limestone, 2 = Andesite, 3 = Sandstone, 4 = Dolomite, 5 = Orthoquarzite.