

Cyanolichen research: a bibliometric analysis from 1991 to 2022

Pesquisa de cianolíquens: uma análise bibliométrica de 1991 a 2022

Investigación de cianolíquenes: un análisis bibliométrico de 1991 a 2022

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Abstract

In the present study, a bibliometric analysis was carried out on cyanolichens, using the ISI Web of Science (WoS) as a database. A total of 244 documents were retrieved, published in the period from 1991 to 2022, and 79 studies published from 2016 to 2022. Considering the entire period analyzed, there was an increase in studies with cyanolichens, with 2013 being the most productive year (21 studies), followed by 2019 (18). The studies were carried out by scientists from 47 countries, with the US, Canada, Germany, Norway and Sweden as the most productive. The bibliometric network of keywords was grouped into four classes: the first and most isolated included taxonomy, evolution and selectivity of symbiotic partners, while the other three classes were associated with ecology, physiology, diversity and conservation of cyanolichens, the latter arranged in a closer relationship, showing that these aspects are often studied together. Analyzing only the period from 2016 to 2022, most of the studies cited show a growing interest in studying nitrogen fixation, functional ecology, associated microbiota and macroevolution of cyanolichens. The bibliometric analysis was effective in demonstrating the state of the art of the study of cyanolichens in a global context, and highlighted the main topics of interest to the scientific community, as well as the countries, researchers, studies and journals that stood out.

Keywords: Lichen-forming fungi; Cyanobacteria; ISI Web of Science; Text mining; Information System Teaching.

Resumo

No presente estudo foi realizada uma análise bibliométrica sobre cianolíquens, utilizando como base de dados a ISI Web of Science (WoS). Um total de 244 documentos foram recuperados, publicados no período de 1991 a 2022, e 79 estudos publicados de 2016 a 2022. Considerando todo o período analisado, observou-se um aumento nos estudos com cianolíquens, sendo o ano de 2013 o mais produtivo (21 estudos), seguido de 2019 (18). Os estudos foram feitos por cientistas de 47 países, com EUA, Canadá, Alemanha, Noruega e Suécia como os mais produtivos. A rede bibliométrica das palavras-chave foi agrupada em quatro classes: a primeira e mais isolada incluiu a taxonomia, evolução e seletividade dos parceiros simbióticos, enquanto as outras três classes foram associadas com ecologia, fisiologia, diversidade e conservação de cianolíquens, estas últimas dispostas em uma relação mais próxima, evidenciando que muitas vezes estes aspectos são estudados juntos. Analisando apenas o período de 2016 à 2022, a maioria dos estudos citados apresentam um interesse crescente em estudar a fixação de nitrogênio, ecologia funcional, microbiota associada e macroevolução dos cianolíquens. A análise bibliométrica foi eficaz em demonstrar o estado da arte do estudo dos cianolíquens em um contexto global, e evidenciou os principais tópicos de interesse da comunidade científica, assim como os países, pesquisadores, estudos e revistas que se destacaram.

Palavras-chave: Fungos formadores de líquens; Cianobactérias; ISI Web of Science; Mineração de texto; Ensino em Sistemas de Informação.

Resumen

En el presente estudio se realizó un análisis bibliométrico sobre cianolíquenes, utilizando como base de datos el ISI Web of Science (WoS). Se recuperaron un total de 244 documentos, publicados en el período de 1991 a 2022, y 79 estudios publicados de 2016 a 2022. Considerando todo el período analizado, hubo un aumento de estudios con cianolíquenes, siendo 2013 el año más productivo (21 estudios), seguido de 2019 (18). Los estudios fueron realizados por científicos de 47 países, siendo Estados Unidos, Canadá, Alemania, Noruega y Suecia los más productivos. La red

bibliométrica de palabras clave se agrupó en cuatro clases: la primera y más aislada incluyó taxonomía, evolución y selectividad de socios simbióticos, mientras que las otras tres clases se asociaron con ecología, fisiología, diversidad y conservación de cianolíquenes, esta última ordenada de manera más estrecha. relación, lo que demuestra que estos aspectos a menudo se estudian juntos. Analizando solo el período de 2016 a 2022, la mayoría de los estudios citados muestran un interés creciente por estudiar la fijación de nitrógeno, la ecología funcional, la microbiota asociada y la macroevolución de los cianolíquenes. El análisis bibliométrico fue efectivo para demostrar el estado del arte del estudio de los cianolíquenes en un contexto global, y destacó los principales temas de interés para la comunidad científica, así como los países, investigadores, estudios y revistas que se destacaron.

Palabras clave: Hongos formadores de líquenes; Cianobacterias; ISI Web of Science; Extracción de textos; Enseñanza en Sistemas de Información.

1. Introduction

Lichens are miniature ecosystems that encompass a main fungus, green algae and/or cyanobacteria, and the associated microbiota, forming a structure called thallus, which can be bipartite or tripartite (Grube et al., 2015; Ramírez-Fernández et al., 2013; Rikkinen, 2015). In bipartite thallus, the fungus is associated with green algae or cyanobacteria; while in tripartite thallus the fungus is associated with both, green algae and cyanobacteria, where the last generally are confined in a structure called cephalodium (Rikkinen, 2015).

Nowadays, approximately 20,000 species of lichenized fungi are known, which only one fifty corresponds to fungi associated with cyanobacteria, and are known as cyanolichens (Hawksworth & Lücking, 2017). The majority of cyanobacteria are *Nostoc* Vaucher ex Bornet & Flahault, formed by cell chains with heterocyst, a structure responsible to the nitrogen fixation. In cyanolichens, the fungi provide physical structure and protection, whereas the cyanobacteria provide fixed carbon and nitrogen. In addition, more than one cyanobacterium lineage can be found within a single cyanolichen species, which seems to be related to the ability of the species to adapt to environmental variations (Rikkinen, 2013, 2015).

The cyanolichens occur in most terrestrial environments, including polar, temperate and tropical areas; especially where the humidity and light incidence requirements are met; and in dry or permanently wet regions there are less diverse (Rikkinen, 2013, 2015). It can develop in different substrates such as rocks, soil, wood, bark and plant leaves; and play important ecological roles, such as in water retention, carbon and nitrogen fixation, and providing habitat for small organisms (Rikkinen, 2013, 2015). Depending to the region of occurrence, the cyanolichens can represent one of the main sources of carbon and nitrogen (Adams et al., 2012), highlighting the importance of these organisms in the world biogeochemistry.

Although important in many ecological aspects, the bibliometric analysis made for cyanolichens research is lacking. The most comprehensive revision regarding cyanolichens can be found in two reviews performed by Jouko Rikkinen (Rikkinen, 2013, 2015), which the general aspects involving the cyanolichen biology, including the cyanobacteria, were presented. The bibliometrics is an approach that uses quantitative methods to analyze and identify patterns in a field of interest, using publications in peer-reviewed journals and books as information source. This method is receiving attention by the scientific community in the last few years, including disciplines such as Biodiversity and Conservation (Liu et al., 2011), health education (Flores-Gomes et al., 2022), environmental remediation (Carvalho Neta et al., 2021), air pollution and effects on the health (Fernandez et al. 2019) and the use of lichens in biomonitoring studies (Abas, 2021). The aim of the present study is to perform a bibliometric analysis of cyanolichen research of the last 31 years.

2. Methodology

For this study, we used the ISI Web of Science (WoS) as the studies repository, made in 31 March (2022), with the term “cyanolichen” searched in all fields. The resulted data was exported in a excel file with the “full register” choice (Supplementary material) in two different datasets: the first with all the publications recovered, and the second with all the publications from the period of 2016 to 2022 (Supplementary material). Information’s such as publications authors and years,

citations and journals names were directly extracted from the resulted file to analyze the data (Supplementary material). The dataset exported was also used in the graphical bibliometric analysis, performed in VOSviewer version 1.6.17 (Van Eck & Waltman, 2010), which is a free software used to graphically present text mining results. In this software, we analyzed the bibliography retrieved from the ISI Web of Science regarding the authors countries and studies key-words for the “all period” dataset.

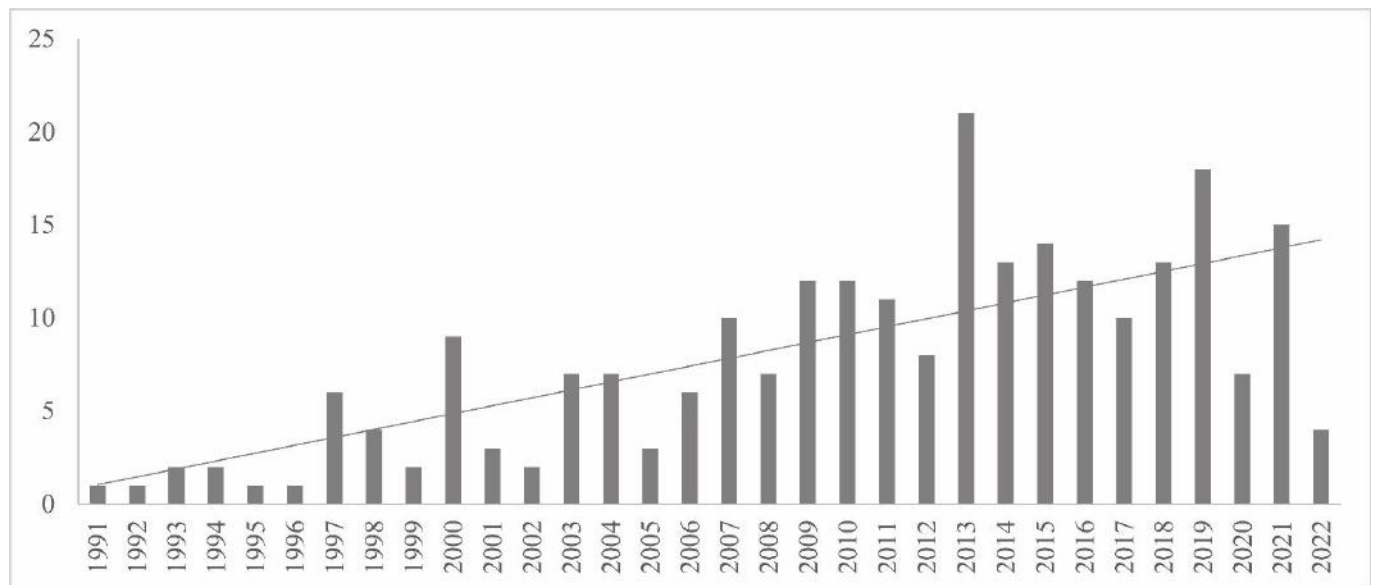
All the key-words were standardized to singular, hyphens were excluded or changed to avoid splitting equal keywords that were written in different ways, in cases such as Lichen – Lichens; Nitrogen-fixation – nitrogen fixation, and others. The key-words had the “5 times cited key-word” cutoff.

3. Results

The search made in March of 2022 for the “cyanolichen” term in the ISI Web of Science (WoS) retrieved 244 studies published between 1991 and 2022, and 79 studies published between 2016 and 2022 (Supplementary material). The first study recorded is the report of the obtention of a well-developed *Peltigera praetextata* (Flörke ex Sommerf.) Zopf from culture, including most of the morphological characteristics observed in natural thalli (Yoshimura & Yamamoto, 1991).

From 1991 to 2022, the cyanolichen research has increased. The year of 2013 presented the higher number of published manuscripts (21 studies), followed by 2019 (18) and 2021 (15) (Figure 1). The studies were published in 113 journals, with the *Bryologist* as the most popular journal (28 studies), followed by *Lichenologist* (18), *Forest Ecology and Management* (12), *Biological Conservation* (7) and *Herzogia* (7) (Supplementary material). In 74 journals, only one cyanolichen manuscript was published (Supplementary material).

Figure 1. Years of publication of the 244 cyanolichens studies retrieved from ISI Web of Science (March 2022).

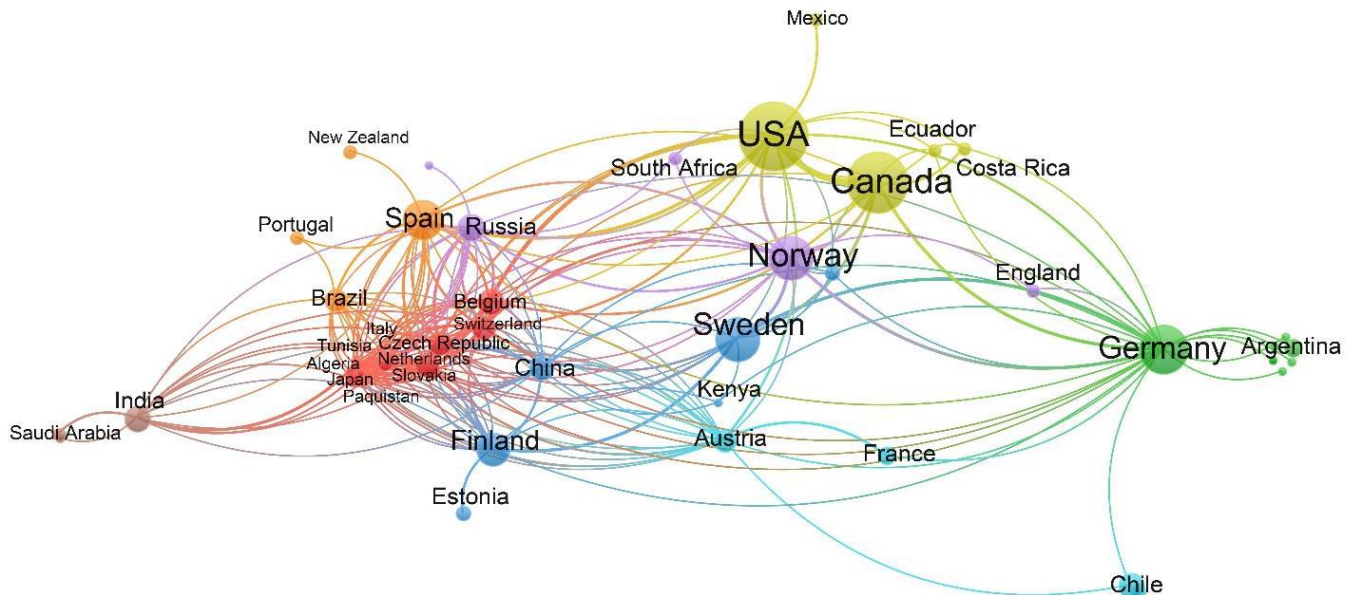


Source: Authors.

The studies were performed by researchers from 47 countries, but Sri Lanka and Iceland were not presented in the figure for the reason that they did not presented link strength (Figure 2). The USA and Canada are the most active countries in publishing manuscripts regarding cyanolichens, with 67 and 50 published studies, respectively, followed by Germany (31 studies), Norway (28), Sweden (28), Spain (19) and Finland (14), with the remaining countries with less than 10 studies published. The countries were clustered in 8 groups, and the group with Algeria, Belgium, Czech Republic, Italy, Japan,

Netherlands, Pakistan, Slovakia, Switzerland and Tunisia was the group that most established connections among countries (marked in red) (Figure 2; Supplementary material).

Figure 2. Collaboration network of the 45 countries that published at least one study with cyanolichens. Colors corresponds to the network clusters. Circles sizes are proportional to the number of publications of each country.



Source: Authors.

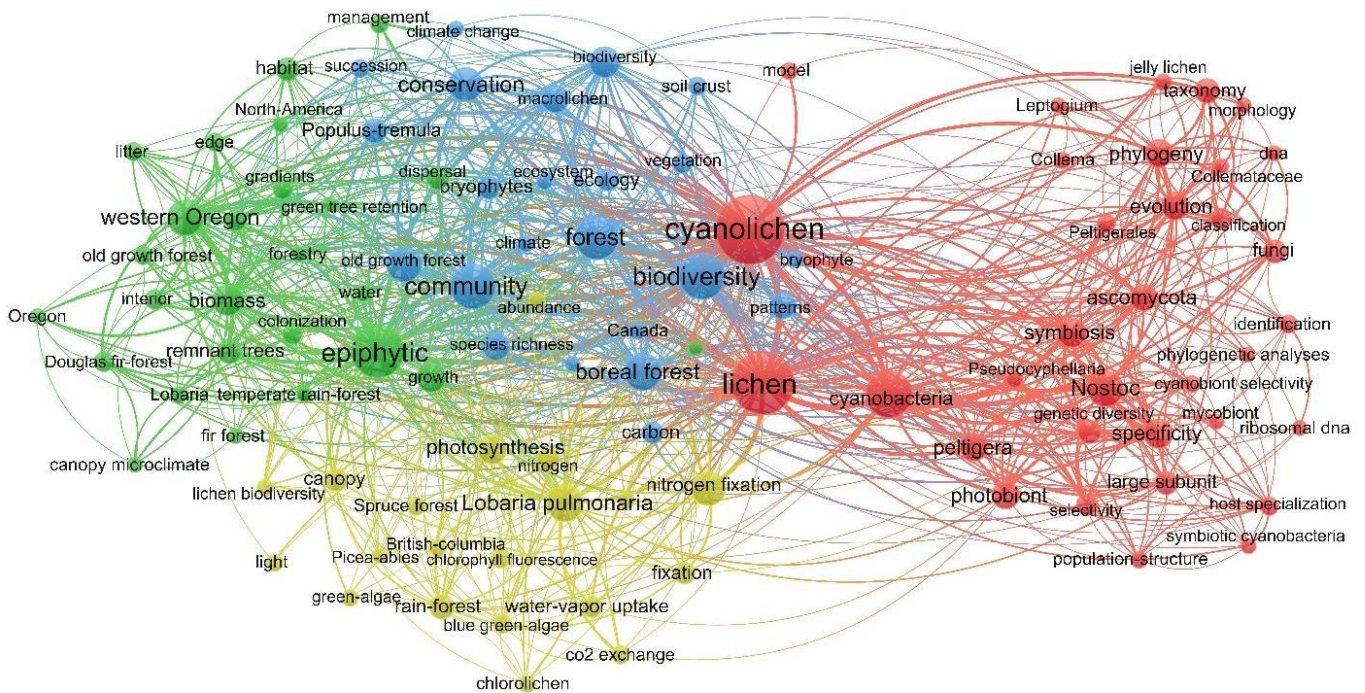
In the 31-years dataset, the 10 most cited studies are found in the Table 1. The revision of Campbell et al. (1998) was the most cited study, with 605 citations, which the cyanolichens were aborred regarding its photosynthesis and acclimation. Then, McCune (1993), with 302 citations, reported the epiphyte biomass in *Pseudotsuga-Tsuga* forests of different ages. The studies of Büdel et al. (2009), Harper and Belnap (2001), and Belnap and Harper (1995), with 198, 162 and 120 citations, respectively, focused in broader contexts such as soil crusts. The study of Harper and Pendleton (1993), with 128 citations, reported the enhance of essential minerals by cyanobacteria and cyanolichens to higher plants in soil samples from National Park, Grand County, Utah, USA. Then, the studies of Neitlich and McCune (1997), Hedenås and Ericson (2000), and Peck and McCune (1997), with 148, 115 and 105 citations, respectively, were focused in epiphytic lichen communities, hotspots and conservation indicators. Finally, Menge and Hedin (2009), with 112 citations, showed that foliose lichens (mainly the cyanolichens of *Pseudocyphellaria*) presented a positive feedback to the ecosystem nitrogen availability.

A total of 1,454 key-words were associated with the 31-years dataset (244 studies), and 103 key-words met the threshold established of “5 times cited key-word” cutoff. The key-words were clustered in four groups, as observed in Figure 3. The first one is involved in studies of taxonomy, classification, evolution and the genetic diversity of the cyanolichen mycobionts and photobionts, including the selectivity and specificity among them (marked in red). The second cluster is related with physiology, such as the role of photobiont in nitrogen-fixation and photosynthesis (in yellow); the third and fourth are related with diversity surveys and conservation studies, including soil crusts (in blue and green).

Regarding the most productive authors of the 31-years dataset (Table 2), Bruce McCune is associated with 16 publications, including three of the ten most cited studies of the 31-years dataset (Table 1). The author is not a specialist in cyanolichens, and work with the biodiversity and ecology of lichens. Other authors, such as François Lutzoni (13 publications), Nicolas Magain (9), Jolanta Miadlikowska (9) and Gregorio Aragón (9) are associated with the most cited studies in the last

seven years (Table 3), and the first three mentioned are frequently working together in many aspects involving the *Peltigera* Willd., in an association between USA and Belgium institutions. Margarita Carú (7) and Julieta Orlando (7), from Chile, have also studied *Peltigera*, including the associated bacterial communities (see Leiva et al., 2016; Ramírez-Fernández et al., 2013; Zúñiga et al., 2017). Gregorio Aragón is also not a specialist in cyanolichens, but his publications are important to understand how cyanolichens functional traits responds to different environments and its patterns on diversity surveys (see Aragón et al., 2010; Benítez et al., 2018; Cardós et al., 2016; Matos et al., 2015; Otálora et al., 2013). Yngvar Gauslaa (13), Art Fredeen (8) and Darwyn Coxson (7) studies, among other topics, lichens ecology and ecophysiology. Matthias Schultz (10) focuses in lichens taxonomy, systematics, biodiversity and evolution and Jouko Rikkinen (10) in interdisciplinary aspects of lichens, including important material of cyanolichen general biology (see for example Rikkinen, 2015) (Table 3 and 4, Supplementary material).

Figure 3. The key-words network of the 30-years dataset. Colors corresponds to the network clusters. Circles sizes are proportional to the frequency of each key-word.



Source: Authors.

When restricting the period of time to seven years (2016-2022) (Table 3), a growing interest in the cyanolichens functional ecology, nitrogen fixation and *Peltigera* macroevolution is observed. For instance, the cyanolichens functional ecology is also explored in a broader context in three studies: Benítez *et al.* (2018), 29 citations; Koch *et al.* (2019), 23 citations; and Jönsson *et al.* (2017), 20 citations. Then, regarding the nitrogen fixation, the revision of Gustafsson (2019) is the most cited manuscript (78 citations), where the cyanolichens were explored regarding its dependence to vanadium in the nitrogen fixation of *Peltigera aphthosa* (L.) Willd., corroborating with Darnajoux *et al.* (2017), which is in fact the third most cited study (35 citations). In addition, the nitrogen fixation of cyanolichens was also aborded in other two of the 10 most cited studies: Zhang *et al.* (2016), with 30 citations; and Darnajoux *et al.* (2019), with 35 citations. For the last, the macroevolution of the *Peltigera* was considered in two studies: Magain *et al.* (2017), 50 citations; and Chagnon *et al.* (2018), 15 citations.

Table 1. The ten most cited studies of the cyanolichen dataset retrieved from ISI Web of Science (WoS) during the period 1991-2022. Cit = number of citations.

Title	Authors	Journal	Year	Cit.
Chlorophyll fluorescence analysis of cyanobacterial photosynthesis and acclimation	Campbell et al.	Microbiology and Molecular Biology Reviews	1998	605
Gradients in epiphyte biomass in three <i>Pseudotsuga-Tsuga</i> forests of different ages in western Oregon and Washington	McCune B.	Bryologist	1993	302
Southern African biological soil crusts are ubiquitous and highly diverse in drylands, being restricted by rainfall frequency	Buedel et al.	Microbial Ecology	2009	198
The influence of biological soil crusts on mineral uptake by associated vascular plants	Harper & Belnap	Journal Of Arid Environments	2001	162
Hotspots of epiphytic lichen diversity in two young managed forests	Neitlich & McCune	Conservation Biology	1997	148
Cyanobacteria and cyanolichens - can they enhance availability of essential minerals for higher-plants	Harper & Pendleton	Annual Meeting of the American-Bryological-and-Lichenological-Society	1993	128
Influence of cryptobiotic soil crusts on elemental content of tissue of two desert seed plants	Belnap & Harper	Arid Soil Research and Rehabilitation	1995	120
Epiphytic macrolichens as conservation indicators: successional sequence in <i>Populus tremula</i> stands	Hedenas & Ericson	Biological Conservation	2000	115
Nitrogen fixation in different biogeochemical niches along a 120.000-year chronosequence in New Zealand	Menge & Hedin	Ecology	2009	112
Remnant trees and canopy lichen communities in western Oregon: A retrospective approach	Peck & McCune	Ecological Applications	1997	105

Source: Authors.

Table 2. The most productive authors of the cyanolichen dataset retrieved from ISI Web of Science (WoS) dataset during the period 1991-2022. RC = Record count.

Authors	RC	Representative study	Institution	Country
Bruce McCune	16	Gradients in epiphyte biomass in three <i>Pseudotsuga-Tsuga</i> forests of different ages in western Oregon and Washington.	Oregon State University	USA
François Lutzoni	13	Multiple origins of high reciprocal symbiotic specificity at an intercontinental spatial scale among gelatinous lichens (Collemaataceae, Lecanoromycetes).	Duke University	USA
Yngvar Gauslaa	13	Rain, dew, and humid air as drivers of morphology, function and spatial distribution in epiphytic lichens.	Norwegian University of Life Sciences	Norway
Jouko Rikkinen	10	Genetic diversity of green algal and cyanobacterial photobionts in <i>Nephroma</i> (Peltigerales).	University of Helsinki	Finland
Matthias Schultz	10	Cyanophilous lichens from Kuwait.	University of Hamburg	Germany
Nicolas Magain	9	Macroevolution of Specificity in cyanolichens of the Genus <i>Peltigera</i> Section <i>Polydactylon</i> (Lecanoromycetes, Ascomycota).	University of Liège	Belgium
Jolanta Miadlikowska	9	Macroevolution of specificity in cyanolichens of the genus <i>Peltigera</i> section <i>Polydactylon</i> (Lecanoromycetes, Ascomycota).	Duke University	USA
Art Fredeen	8	Importance of arboreal cyanolichen abundance to nitrogen cycling in sub-boreal spruce and fir forests of Central British Columbia, Canada.	University of Northern British Columbia	Canada
Gregorio Aragón	7	Effects of forest management on epiphytic lichen diversity in Mediterranean forests.	King Juan Carlos University	Spain
Margarita Carú	7	Phylogenetic diversity of <i>Peltigera</i> cyanolichens and their photobionts in Southern Chile and Antarctica.	Universidad de Chile	Chile

Source: Authors.

Table 3. The ten most cited studies of the cyanolichen dataset retrieved from ISI Web of Science (WoS) during the period 2016-2022. Cit = number of citations.

Title	Authors	Journal	Year	Cit.
Vanadium geochemistry in the biogeosphere -speciation, solid-solution interactions, and ecotoxicity.	Gustafsson, JP.	Applied Geochemistry	2019	78
Macroevolution of Specificity in cyanolichens of the genus <i>Peltigera</i> Section <i>Polydactylon</i> (Lecanoromycetes, Ascomycota).	Magain et al.	Systematic Biology	2017	50
Biological nitrogen fixation by alternative nitrogenases in boreal cyanolichens: importance of molybdenum availability and implications for current biological nitrogen fixation estimates.	Darnajoux et al.	New Phytologist	2017	35
Alternative nitrogenase activity in the environment and nitrogen cycle implications.	Zhang et al.	Biogeochemistry	2016	30
Functional traits of epiphytic lichens in response to forest disturbance and as predictors of total richness and diversity.	Benitez et al.	Ecological Indicators	2018	29
Selecting lichen functional traits as ecological indicators of the effects of urban environment.	Koch et al.	Science of the Total Environment	2019	23
Molybdenum threshold for ecosystem scale alternative vanadium nitrogenase activity in boreal forests.	Darnajoux et al.	Proceedings of the National Academy of Sciences of the United States of America	2019	22
Will forest conservation areas protect functionally important diversity of fungi and lichens over time?	Jonsseton et al.	Biodiversity and Conservation	2017	20
Fungal Systematics and Evolution: FUSE 4.	Liu et al.	Sydowia	2018	17
Strong specificity and network modularity at a very fine phylogenetic scale in the lichen genus <i>Peltigera</i> .	Chagnon et al.	Oecologia	2018	15

Source: Authors.

4. Discussion

The cyanolichens research is receiving a growing interest from the scientific community in the 21st century. The publications are mainly concentrated in five journals, and the researchers from USA and Canada are the most active in publishing studies with cyanolichens, although other countries, such as Algeria, Belgium, Czech Republic and others are establishing more international connections. The key-word analysis shows that the taxonomical studies are focused mostly in the species circumscriptions, selectivity and specificity among bionts, which can be graphically observed with the separation of the first cluster (in red) from the remaining, while the other four clusters are involved in interdisciplinary studies, with many connections among them (Figure 3).

The recent most cited studies shows that the functional traits, nitrogen fixation and aspects involving the cyanolichens macroevolution patterns are actually being explored nowadays, and the general findings regarding each topic are explored in the trends in cyanolichenology section. In addition, other two subjects published recently with the participation of some of the most relevant researchers are also mentioned: cyanolichens bacterial communities; and the interactions between cyanolichens mycobiont and photobiont in tropical montane forests

Trends in Cyanolichenology

4.1 Cyanolichens functional traits

The research of the lichen's functional trait variations, for example the type of photobiont, growth forms and reproduction strategies, are a cost-effective alternative to assess the response of communities to ecological gradients, land use, forest disturbance, fragmentation and urbanization; once those traits are related with biotic and abiotic factors such as water

availability, temperature, light intensity and many others. Recent studies regarding the cyanolichens functional ecology found response patterns to different environmental conditions (Benítez et al., 2018; Golovko et al., 2020; Jönsson et al., 2017; Koch et al., 2019; Nimis et al., 2020; Phinney et al., 2022). For instance, along a gradient of aridity and light intensity in Italy, cyanolichens were morphologically “simpler” (crustose growth-form and sexually reproducing) in dry habitats on calcareous rocks, and were gradually replaced to “more complex” species (often asexual such as foliose sorediate) until humid and shaded habitats on tree bark (Nimis et al., 2020).

In Norway, the cyanolichens photobiont type and reproductive mode were associated with biogeographical patterns: The trebouxoid species reached its peak in colder and drier regions, while the trentepohlioid lichen species were associated with wetter and warmer climatic conditions. Meanwhile, the sorediate and isidiate species were positively related to the temperature. In general, the cyanolichens increased their diversity with the increase in precipitation, reaching its peak in coastal areas (Phinney et al., 2022).

In tropical montane forests from southern Ecuador, the occurrence of lichen species with cyanobacteria and gelatinose growth form decreased when increased the forest disturbance, occurring mainly in remnants of primary forest fragments and reducing in secondary forest fragments regenerated after logging (Benítez et al., 2018). In boreal old-growth forest key habitats from central Sweden, the cyanolichens frequency reduced even in conserved areas, possibly because the area is part of a severely fragmented landscape (Jönsson et al., 2017).

In urban areas of Southern Brazil, cyanolichens showed higher relative frequency in zones of lower urbanization density (Koch et al., 2019). The authors raised the possibilities that the high capacity of cyanolichens to retain water may facilitate the deposition of pollution and restrict their occurrences in disturbed areas, or/and areas with high degree of urbanization may suffer with more intensity the “urban heat island” effects, which is characterized by lower humidity and higher temperatures that limit the occurrence of cyanolichens (Bargagli & Mikhailova, 2002; Koch et al., 2019).

4.2 Nitrogen-fixation

The Biological Nitrogen Fixation (BNF) is the main route for input fixed nitrogen in the unmanaged terrestrial ecosystems, which is a result of prokaryotes nitrogenase enzyme activities, including the main, molybdenum dependent nitrogenase (Mo-Nase), and the vanadium (V-Nase) and iron (Fe-Nase) dependent nitrogenases (Gustafsson, 2019; Zhang et al., 2016). However, there are limitations on the availability of molybdenum in different regions of the planet (see the review performed by Bellenger et al., 2020), and due to this, it was hypothesized that the vanadium (50-200 times more abundant than molybdenum) and V-Nase activity could also play an important role in BNF (Darnajoux et al., 2014). Darnajoux *et al.* (2014) searched for the vanadium and molybdenum homeostasis in the *Peltigera aphthosa*, a tripartite species with the cyanobacterium (*Nostoc*) confined in the cephalodia structure. The authors found a higher concentration of vanadium and molybdenum in the cephalodium structure than in the photobiont portion of the thallus, reflecting the importance of both biometals to the nitrogen fixation by *Nostoc*. Later, Darnajoux *et al.* (2017) confirmed that the vanadium is biological important to *P. aphthosa* s.l. throughout the boreal biome, and also that the molybdenum availability plays a role in the regulation of vanadium inside the *P. aphthosa* s.l. *Nostoc* structure. This was also confirmed for many other *Peltigera* of high latitudes, where the V-Nase activity presented a strong inverse correlation with the molybdenum content of *Peltigera* thalli, confirming the hypothesis that vanadium is important to BNF where the molybdenum availability is limited (Darnajoux et al., 2019).

4.3 Interactions between cyanolichens mycobiont and photobiont in tropical montane forests

In southern Kenya, 74 different species of cyanolichens (Peltigerales) were associated with 393 *Nostoc* lineages, 156 of the *Nephroma*-type group and 237 of the *Collema/Peltigera*-type group. Among the mycobionts, 58% lineages shared its photobiont with at least one other mycobiont, showing the presence of both generalist and specialist lineages. The taxa with apothecia were more generalist with their photobiont than the species lacking apothecia or with vegetative structures reproduction (Kaasalainen et al., 2021), which corroborate with the hypothesis that symbiotic dispersing lichens may facilitates the re-establishment of sexually dispersing species (Belinchón et al., 2015; Kaasalainen et al., 2021; Svensson et al., 2016).

4.4 *Peltigera* and *Nostoc* macroevolution

Among the 70 manuscripts with cyanolichens published in the last five years, 18 (approx. 26%) exclusively addressed hypothesis regarding the *Peltigera*, with many aspects, such as the genera evolution, diversification, selectivity among bionts, ecology, microbiota, and other topics explored (Supplementary material 1).

For example, Magain *et al.* (2017) selected the *Peltigera*, section *Polydactylon*, to study the macroevolution and specificity of cyanolichens symbiotic partners. Five nuclear loci and the *rbcLX* region were used to infer the mycobionts and *Nostoc* phylogenies from samples collected worldwide, revealing a broad spectrum of specificity among partners and also new species, with 38 well-delimited lineages among 14 previous *Peltigera* names, which were associated with 25 *Nostoc* phylogroups. In general, the authors found that: a) specialist mycobiont lineages (associated with one or few *Nostoc* lineages) are older, less genetic diverse and presents a narrower geographical distribution; while b) generalist mycobiont lineages are younger and presents higher genetic diversity, which seems to be advantageous to the expansion of geographical range distribution, as they present wider distribution. Also, c) the mycobionts are more specialists when compared with *Nostoc*, that frequently are associated with several *Peltigera* species; d) the *Nostoc Peltigera*-associated phylogroups also contains lineages associated with other lichen-forming groups and even with plants; and e) the patterns of bionts selectivity are structured geographically, ecologically and phylogenetically.

At local scale (Québec, Canada), Lu *et al.* (2018) corroborated with the asymmetric specificity among bionts of *Peltigera* species, with specialized mycobiont associated with generalist photobionts, but the geographical distributions of generalists were not higher than specialists as observed in Magain *et al.* (2017). In this study, the authors found that environmental factors, such as precipitation, also influence the species distribution in boreal areas (Lu et al., 2018). In Estonia, Jüriado *et al.* (2019) found that beyond the mycobiont identity, habitat preferences also play an important role in *Nostoc* selectivity, indicating a functional structuration within the photobiont communities.

Contradictorily, Chagnon *et al.* (2018) performed network analyses of the *Peltigera*, section *Polydactylon*, at global and local (British Columbia, Canada) scales, and found that the *Nostoc* lineages of a thallus was best predicted by the mycobiont identity, while the influence of the region or biome of the thallus remained marginal. Later, Chagnon *et al.* (2019) suggested that the maintenance of high levels of mycobiont specialization is a result of speciation events, that were occasioned by the process of a novel partner acquisition, followed by the loss of the ancestral one.

4.5 Cyanolichens bacterial communities

In the last years, the bacterial communities that are associated within a lichen thallus have been studied. In fact, they have become recognized as a component of the symbiosis and plays important roles in lichen physiology (Grube et al., 2009, 2015). The aspects regarding what shapes the bacterial communities' structure such as the mycobiont identity, photobiont type, geography and ecology have been explored, but more extensively regarding clorolichens (e.g. Grube et al., 2009; Hodkinson et al., 2012). With the cyanolichens, Ramírez-Fernández *et al.* (2013) studied the bacterial community associated with *Peltigera*

species and from their respective substrates in three habitats from Tierra del Fuego (Chile). The authors found differences between the sample sources, showing that the cyanolichen microbiota is not a merely continuation of the substrate microbiota. The same was found by Almendras *et al.* (2018) which the nitrogen-fixing bacteria associated with bipartite *Peltigera* were different from those present in their substrates, located on a secondary forest of *Nothofagus pumilio* in the Coyhaique National Reserve, Chile.

Leiva *et al.* (2016) found that the bacterial microbiota on the substrate of *Peltigera* species were different according to the cyanobiont identity, which indicates that the cyanobiont metabolites influence the soil nutrient availability. Recently, Leiva *et al.* (2021) proposed that *P. frigida* may carry its own bacterial communities when propagating, but also that the species acquire a part of the bacterial community from the substrate.

The bacterial communities of the marine cyanolichens *Lichina confinis* (O.F. Müll.) C. Agardh and *L. pygmaea* (Lightf.) C. Agardh, collected in the Brittany coast (France), were searched by the Illumina sequencing approach of the 16S rRNA region. As results, the distribution and relative abundance of the bacterial community were significantly different within each species, although with overlapping that can be related with a potential adaptation to their habitats in different littoral zones. For instance, *L. confinis* occurs in the upper eulittoral zone and is more exposed to the air, higher temperatures and UV radiation; while *L. pygmaea* occurs in lower eulittoral zone and is immersed in the sea half of day. The differences among the species bacterial communities are a response to the habitat pressure that each species is exposed, e.g. in *L. confinis* microbiota were found groups that can be associated with UV radiation protection, while *L. pygmaea* had bacteria that can be associated with salt stress acclimatation (West *et al.*, 2018).

5. Final Considerations

The bibliometric approach showed to be a good tool to access the current state of art of the cyanolichens research and inferred subjects that has been discussed by the scientific community. Although the publications regarding cyanolichens did not begin with the first record recovered, and that all publications regarding these organisms were not included in our study due to WoS limitations (see Martín-Martín *et al.*, 2021), the present study revealed interesting aspects of cyanolichens research. Many other sources of citations such as Google Scholar, Microsoft Academic, Scopus and Dimensions should be included in future studies regarding lichenized fungi in general.

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