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Overview of Lichen

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1.1 Introduction

The term “lichen” was coined by Theophrastus (Father of Botany) more than two thousand years ago. Till the 19th century, lichens were thought to be individually recognized organisms. In 1869, only it was accepted that it was composed of two different organisms [1, 2]. Lichens are composed of different species of fungi (Mycobiont), algae, or cyanobacteria (Photobiont) [3–9], and some microorganisms like bacteria are also associated with them [10–14]. There is a long debate and study regarding the combination of association of different components of lichen symbiosis and their physiology [15–17]. Though lichen is composed of different components, they form morphologically constant forms that are designated as species [18]. They are frequently specified as the best example of mutualistic partnerships. Photobionts have the capacity to photosynthesize; they provide carbohydrates to the fungal partner, and the mycobiont creates a physical scaffold that encloses and supports the growth of photobionts [5]. According to Hawksworth, “a lichen is a stable self-supporting association of a mycobiont and a photobiont in which mycobiont is the exhabitant” [4]. Through a process called lichenization, a fungus and a photosynthetic partner transformed into a lichen thallus, from a free-living to a symbiotic state [19].

Lichens are distributed throughout the world and found to grow in almost all climatic conditions (“Lichens,” [20]). They are dominating the earth’s terrestrial ecosystem, particularly in the subarctic and arctic regions, covering about 8–10% of the total area [21]. About 13,500–20,000 species of lichens have been recognized globally so far [22–25]. According to the Botanical Survey of India, 19,500 species have been discovered so far (“Lichens,” [20]). Lucking et al. made a prediction, which is 26,000 lichen taxa [26]. Among approximately 20,000 species of lichen-forming fungus known to exist worldwide, Ascomycetes make up 98% of all known lichenized fungi, followed by Deuteromycetes (1.6%), and Basidiomycetes (0.4%). On the other hand, there are only roughly 156 species of photobionts across 56 taxa. The majority of photobionts are either cyanobacteria (Cyanoprokaryota-35 species, 22.3%)

or green algae (Chlorophyta-116 species, 73.9% of total photobiont diversity). The three most common photobiont genera in lichens are *Trebouxia*, *Trentepohlia*, and *Nostoc* [5].

Lichens are separated into two groups based on their size: macrolichens and microlichens. They are classified as corticolous, ramicolous, lignicolous, saxicolous, muscicolous, terricolous, and foliicolous based on the substrate on which they develop. They are also separated into three groups based on their physical characteristics: foliose, fruticose, and crustose [27]. Anatomically, the majority of lichen thallus is stratified into the upper cortex, photobiont layer, medulla, and lower cortex. The cortex of many foliose and fruticose lichens is made up of pseudoparenchymatous or prosoplectenchymatous tissues of fungi. The medullary layer consists of loosely interwoven long-celled hyphae having internal airspace. The photobiont layer is formed by the upper part of the medulla. Crystalline secondary products often encrusted the hyphal cell walls of the algal and medullary layers. The lower cortex is well-developed in some typical foliose lichen groups like Parmeliaceae. Reproduction of lichen is mainly expressed by its fungal partner with sexual and asexual methods, while it is reduced in case of the algal partner in the lichenized state [28].

The significant role played by lichens includes natural soil formation and nutrient cycling [29]. For monitoring anthropogenic disturbances over time, such as air pollution, acid rain, nitrogen deposition, and several other environmental variables, lichens have been utilized as a crucial biological indicator [7, 30]. Since long time, a wide range of lichen species have been used as traditional medicine and in different folk cultures in countries like North America, Europe, India, Nepal, and China [31–35]. They are also good sources of human food and are also taken by various wild and domesticated animals as feed, containing a range of nutrients and biologically active compounds [36–38]. Some lichens are also used as raw materials in various industries like cosmetics and perfume, minerals, brewing, distilling, and essential oil [32, 38].

The globally declining trends of abundance and diversity of lichens have been documented by various authors across the world. Pollution due to industrialization, large-scale modern agriculture, urbanization, deforestation, habitat loss, overexploitation, global warming, and climate change are the main causes of their decline [22, 39].

1.2 Distribution

Lichens have some surprising capacity of ecological resilience and adaptability. They can absorb and retain moisture from various sources, due to which they can easily grow in exposed substratum like leaves and barks of trees, rocks, etc., and can survive in extreme conditions like hot deserts, barren rocky cliffs, and frozen environments of the polar regions. They can also grow in the marble of old buildings and monuments [5, 25].

Lichens are an old group of fungi that may be traced back to 400 MA to the Early Devonian in the Rhynie chert deposits in Scotland and to 600 MA in marine phosphorite of the Doushantuo Formation at Weng'an in South China. The earliest ascomycetes may symbiotically associate with the already available algae and cyanobacteria, which formed the hypothetical *Protolichen* group. Eighteen (18) patterns of lichen distributions are described by Galloway, which are Cosmopolitan, Endemic, Austral, Bipolar, Paleotropical, Neotropical,

Pantropical, Australasian, Circum-pacific, Atlantic, Eastern North America–western European (amphi-Atlantic), Western North American–western European, Mediterranean, American–Asian, South American–African, Southern xeric and Boreal arctic–alpine taxa [40]. The cosmopolitan taxa are widespread in their occurrence and found in all land masses and various oceanic islands. The family Parmeliaceae has a worldwide distribution having species like *Parmelia sulcata*, *Flavoparmelia caperata*, *Hypotrachyna sinuosa*, *Parmotrema perlatum*, etc. The endemic lichen taxa are present in some particular geographical areas with limited distribution. Lichen flora of India comprises over 2900 species, among which 18% (540 species) are endemic. (“Lichens,” [20]). In New Zealand, 23% of their lichen flora is endemic. Some of the endemic lichen species of New Zealand are *Austrella brunnea*, *Caloplaca erecta*, *Lobaria asperula*, *Umbilicaria murihikuana*, etc. A high percentage of endemic lichen flora is found in South Georgia (24%) to continental Antarctica (50%). The Austral taxa are represented by the southern hemisphere land masses, and the lichen flora is divided into Paleoaustral and Neoaustral lichens. The Paleoaustral lichens are represented by the primitive Gondwanan groups, which are poorly adapted for long-distance dispersal; examples are—*Bartlettia fragilis*, *Brigantiaea phaeomma*, *Bryoria austromontana*, *Caloplaca cribrata*, etc. The Neoaustral lichens are dispersed after Gondwanaland fragmentation, which takes place between the post-Oligocene and the present. Some examples of Neoaustral lichens are—*Caloplaca cirrochroides*, *Leifidium tenerum*, *Parmelia cunninghamii*, etc. The lichens which are distributed in high latitudes of both the northern and southern hemispheres are the bipolar taxa. Some examples of bipolar lichen taxa are *Cladonia ecmocyna*, *Caloplaca tornoensis*, *Bellemera alpine*, etc. The lichen flora found in Africa, the Indian subcontinent, the Arabian peninsula, the Malesian Archipelago, and some islands of the Pacific Ocean are called Paleotropical taxa. *Bactrospora metabola*, *Cladia aggregate*, *Parmelinopsis swinscowii*, etc., are examples of Paleotropical taxa. The lichen species represented in some regions of South America and the Caribbean islands are known as Neotropical taxa. Some of the Neotropical lichen taxa are species of *Erioderma*, *Leptogium*, and *Peltigera*. Pantropical taxa are found in most of the tropical regions and show affinities with warm temperate characteristics, for example—species of *Parmotrema*, *Glyphis*, *Graphis*, etc. Australasian lichen taxa have similar characteristics to the lichen flora represented in Australia and New Zealand. Species of the genus *Nothofagus*, *Placopsis*, are included in the Australasian taxa. The Western Pacific lichen taxa are found in the extent northwards to Japan, westwards to India, and in some parts of Africa of Australia. *Calopadia subcoerulescens*, *Parmelia erumpens*, and *Rinodina reagens* are some examples of Western Pacific lichen taxa. The lichens found to grow around the Pacific Ocean are called Circum-Pacific taxa, for example—*Hypogymnia pulverata*, *Placopsis cribellans*, *Mastodia tessellate*, etc. The Atlantic lichen taxa are found in the islands of the Atlantic Ocean. Some Atlantic taxa are—*Byssoloma croceum*, *Pyrenula hibernicum*, *Porina atlantica*, etc. Lichen flora of present-day North Atlantic regions are known as Eastern North America–western European or amphi-Atlantic taxa. Comparatively, fewer lichen species are distributed in this region, some of them are *Cladonia strepsilis*, *Rhizocarpon timdalii*, *Lasallia pustulata*, etc. Various lichen taxa are restricted to the areas of western North America and Western Europe, for example—*Cliostomum leprosum*, *Lecidella laureri*, *Rinodina disjuncta*, etc. The Mediterranean lichen taxa are comprised of characteristics of different elements—northern, temperate, humid sub-tropical element, and arid. Some of the lichen species found in this

region are *Diploschistes diacapsis*, *Placidium fringens*, *Toninia tristis*, etc. The lichens are represented in the regions of eastern North American–eastern Asian pattern called American–Asian taxa, which are—species under the genus *Cetrelia*, *Collema*, *Allocetraria*, etc. The South American–African taxa of lichen are isolated between South America and southern Africa. Some of the lichen flora of this type are—*Peltula clavata*, *Umbilicaria haplocarpus*, *Caloplaca isidiosa*, etc. The Southern xeric taxa are distributed in the regions of southern Africa, Western Australia, South Australia, and southern New Zealand with characteristic climatic conditions like winter rainfall and summer drought. *Diploschistes hensseniae*, *Xanthoparmelia subimitatrix*, *Digitothyrea rotundata*, etc. are some of the species recorded under this region. The boreal arctic-alpine taxa are confined to the areas of the northern hemisphere, such as North America, Europe, and some parts of Asia. The lichen species found in this region are mostly growing in woodlands, heathlands, and tundra. Some of the lichen species found in this region are under the genus—*Cladonia*, *Cetraria*, *Vulpicida*, *Brodoa*, etc. [40].

Although the distribution range sizes and patterns of many lichen species resemble those of vascular plants, lichens have far more continental disjunctions. Species of “enigmatic disjunctions” are primarily characterized by having rather large distributional areas in each of the continents where they occur. An even more enigmatic portion of this group of disjunct species exhibits a normal-sized distributional area in one or more continents but an extremely restricted, point-like distribution in another. For example, *Alectoria imshaugii* grows in large areas of the west coast of North America from south Alberta to northeast California but is only known from Gomera to Hierro in the Canary Islands in Africa. *Cetraria odontella*, commonly found in Finland and Sweden has a holarctic distribution that can also be found on Australia’s Mount Kosciusko. A most extreme type of enigmatic disjunct distribution is shown by *Coleopogon abraxus*, which was only known from a mountain on the east coast of Cape Town, South Africa, but has recently been observed in a forest of central Chile. Another species, *Acroscyphus sphaerophoroides*, is found to grow in 13 different areas of Bhutan, China, Canada, Japan, Patagonia, Peru, South Africa, and the United States [23].

1.3 Morphology and Anatomy

In most of the lichen, the fungal partner mainly determines the morphological appearance. In only a few lichen thallus, it is determined by the algal partner. There are three morphological groups of lichens based on their habit—crustose, foliose, and fruticose [28, 41, 42]. The simple and undifferentiated thallus, with irregularly distributed algae, are known as homioimerous, and more complex thallus, where algae are restricted to a particular layer in the thallus and medullas without algae are called heteroimerous.

In crustose lichens, the thallus is tightly attached to the substratum and is difficult to detach from the surface. In most cases, the thallus contains a well-defined upper cortex, an algal layer, and a medulla. There are various subtypes of crustose lichens—powdery, endolithic, endophloeodic, squamulose, peltate, pulvinate, lobate, effigurate and suffruticose crusts. The powdery crusts or leprose type thallus are simple in structure, where fungal hyphae cover algal cells, and they have no definite algal or fungal layer, e.g. *Lepraria* genus.

The endolithic lichen (e.g. *Acrocordia conoidea* and *Verrucaria baldensis*) grows inside rock, while endophloeodic lichens grow underneath the cuticle of leaves and stems of higher plants. They are more organized in structure and form an upper cortex consisting of a densely conglutinated hyphal layer named “lithocortex.” In the squamulose type of crustose lichen, the areolae are enlarged in the upper portion and become partly free from the substrate, often form overlapping scale-like squamules (e.g. genera like *Catapyrenium* and *Peltula*). In general like *Mobergia*, squamules are extremely inflated; they are called bullate type. The peltate type has more or less central attachment area on the lower surface of flat scales of squamulose thalli (e.g. *Peltula euploca* and *Anema nummularium*). In effigurate type of thallus, the marginal lobes are prolonged and are radially arranged, e.g. genera like *Caloplaca* and *Acarospora*. When the thallus becomes radially striate with marginal lobes, they are called lobate type of thallus [28].

The foliose lichens are flat and leaf-like, partially attached to the substratum. They have well-defined upper and lower surfaces with dorsiventral organization. The branching thallus bears several lobes. The foliose lichens may be of two types—lacinate and umbilicate. Lacinate lichens are lobate with various sizes. In *Parmelia* species, the lobes are radially arranged, and in *Peltigera*, lobes overlap, similar to tiles on a roof. In *Menegazzia*, thallus lobes are inflated with a hollow medullary center. Umbilicate lichen thallus is circular in look and consists of either one single unbranched lobe or a multilobate with a limited branching pattern. Umbilicate type of thallus has a central umbilicus, which arises from the lower surface and is attached to the substratum.

In Fruticose lichens, the thallus lobes are hair-like, strap-shaped, or shrubby; lobes are either flat or cylindrical. In some of the fruticose lichens, thallus is dorsiventrally arranged, e.g. *Evernia prunastri*. Some of them have radially symmetrical thalli, e.g. *Usnea* and *Ramalina* species [28].

The cortex is the outermost protective layer of stratified lichen thallus. In some foliose lichen, the cortex may also be present in the lower side of the thallus but is absent in the squamulose type. The photobiont layer of stratified lichen is formed just beneath the cortex. The medulla occupies most part of the thallus in stratified lichen composed of fungal hyphae.

1.4 Reproduction

In a lichenized state, the fungal partner usually expresses full sexual and to a certain extent, asexual mode of reproduction, whereas in the case of an algal partner, it is a reduced type [28]. Since lichen cannot exist without the symbiotic relationship between a mycobiont and a photobiont, either both partners must be dispersed at the same time, or specific adaptations must guarantee contact and relichenization following the independent dispersal of mycobionts and photobionts. The lichen’s symbiotic relationship allows it to thrive on a broad range of substrates under a range of climatic circumstances, but its primary means of dispersal—sexual or non-sexual—is determined by its mode of reproduction. After being released, the fungal spores germinate on an appropriate substrate, take up algae that are compatible with them, and grow new vegetative thalli. Mycobionts and photobionts coexist and reproduce to produce vegetative propagules such hormocysts, isidia, and soredia.

Even the typical means of propagation that photobionts experience in their free-living stage may be absent or extremely limited in lichenized conditions.

In lichens, one of the most common forms of vegetative reproduction is fragmentation. There is the potentiality to act as a source of regeneration of any portion of lichen thallus containing both the symbionts. The soredia are formed in specialized organ soredia; they are the most common diaspore of foliose and fruticose lichen. Another diaspore is formed by isidia, which are finger-like projections with well-developed fungal tissue enclosed by algal cells. They are very commonly found in crustose, foliose, and fruticose lichen species. When the photobiont is a cyanobacteria, hormocytes are formed, which consist of trichomes or individual cells with a gelatinous sheath [43]. The sexual reproduction of Ascomycetes and Basidiomycetes fungi as a lichen partner is analogous to that in free-living Ascomycetes and Basidiomycetes [44].

1.5 Lichen Phytochemicals

The secondary metabolites produced by lichen are known as lichen phytochemicals [45]. All these phytochemicals are of fungal origin [46]. Other than primary metabolites (proteins, amino acids, polyols, carotenoids, polysaccharides, and vitamins), lichen also produces over 700–1050 (including under culture) different secondary metabolites. The main categories of lichen phytochemicals are depsides, depsidones, dibenzofurans, anthraquinones, xanthenes, chromones, pulvinic acid derivatives, terphenylquinones, terpenes and steroids. The medulla portion of lichen thallus mostly produces colorless depsides and depsidones. Usnic acid is also formed in the medulla portion [25, 47].

Lichen phytochemicals play some important ecological and medicinal roles, which determine the relative ecological success of individual lichen species. In lichen thallus, these phytochemicals are responsible for light-screening, chemical withering, biological defense, anti-herbivore defense, and allergenic. The yellow-colored cortical pigment, usnic acid is produced by thousands of lichen that are exposed to the sun, while the lichen containing a low concentration of depsides is grey-green in color and shade loving [48]. Many lichen substances exhibit multiple biological activities, such as the dibenzofuran usnic acid, which has characteristic antimicrobial, larvicidal, and anticancer properties, and is also known for its ultraviolet absorption. The phytochemicals are genetically regulated and, in certain cases are related to an individual's morphology and location within a species or genus. Since secondary metabolite distribution patterns are typically species-specific, they are frequently employed in lichen systematics and taxonomy. Secondary metabolites from lichens can act as allelopathic agents, which means they can have an impact on the growth and development of nearby lichens, mosses, and vascular plants as well as microbes. Some lichens can significantly inhibit the growth of higher plants. It has been demonstrated that two common species found in boreal forests, *Cladonia stellaris* and *Cladonia rangiferina*, exhibit allelopathic effects on white spruce and jack pine (*Pinus banksiana*) [25].

The most studied lichen substance is usnic acid, which was isolated in 1884 from *Usnea* and later from other lichen genera- *Cladonia*, *Hypotrachyna*, *Lecanora*, *Ramalina*, *Evernia*, *Parmelia* and *Alectoria*. Usnic acid is famous for its anti-proliferative activity and has anticancer potential. Cellular apoptosis (programmed cell death) of carcinogenic

cell lines observed after treatment of usnic acid. It has the ability to affect cell lines of ovarian, hepatic, gastric, and breast cancer. Another compound atranorin extracted from some lichen species like *Everniastrum vexans* was tested for its anticancer properties. Regarding toxicity studies in the human body, there are some records in case of usnic acid [49].

1.6 Economic Importance

Lichens are good sources of food for humans and feed for other animals. *Cetraria islandica*, *Lecanora esculenta*, *Umbilicaria esculenta*, *Peltigera canina*, *Parmelia* sp., and *Ramalina sinensis* are consumed as food in different countries. *Cladonia rangiferina*, *C. rangiferina*, *Cetraria islandica*, species of *Parmelia*, *Evernia*, etc., are used as fodder in many countries. Some of the lichen species are used as flavoring agents, e.g. *Heterodermia tremulans*, species of *Pyxine*, *Physcia*, etc. Some lichen species are commercially used in the Litmus dye industry. Litmus mixture is obtained from *Roccella tinctoria*. Moreover, they are also used in the textile dye industry. Red-colored natural dye is obtained from *Rubia tinctorum* and *Rubia cordifolia*. *Evernia prunastri* has been used for making perfume and the cosmetic industry.

There are several lichen species that have medicinal properties, such as antimicrobial, antiviral, anti-inflammatory, anticancer, insecticidal, antipyretic, etc. *Usnea* sp. (anti-cancer), *U. esculenta* (anti-HIV), *Parmelia* sp. (wound healing), etc., are some medicinal lichens [37]. Scientific investigations have identified a large number of lichen species, indicating their biological activity and application in traditional medicine. About 60 lichen genera that have been traditionally employed by various cultures worldwide, primarily in North America, Europe, and Asia. Traditionally, the most commonly used lichen genera is *Usnea*, which is used around the world. The lichen genera *Cladonia*, *Ramalina*, *Lobaria*, *Peltigera*, *Evernia*, *Pseudevernia*, *Umbilicaria*, *Xanthoparmelia*, *Letharia*, *Cetraria*, *Parmotrema*, *Thamnolia* are used for various medical conditions like external injuries, skin infections, respiratory ailments, etc. *C. islandica* has been used in European pharmacopoeias to treat lung disease, cold symptoms, and gastroenteritis since 1500. *Pseudevernia furfuracea* was used by the Egyptians in the process of embalming mummies for aromatic purposes and is now effectively used in the perfume industry. In India, *Usnea longissima* has been used in traditional medicine for its analgesic, cardiogenic, digestive, and wound-healing properties [49].

Due to their sensitivity to various pollutants (nitrogen, sulfur, etc.) and heavy metals, lichens are widely recognized as bioindicators of environmental pollution. The health condition of lichen can indicate the accumulation of heavy metals showing its negative effect [25, 29].

1.7 Conservation

The rate of species extinction in the Anthropocene has been 100–1000 times higher than the background rate, or 0.1–1 million species per year. They have coincided with reductions in the useful biodiversity [50]. Experts in biodiversity calculated that since 1500, over

30% (uncertainty range: 16–50%) of species have faced worldwide threats or have been driven extinct. Habitat loss and climate change are predicted to worsen the extent of biodiversity loss. According to expert estimates, either 41% (range: 30–60%) or 80% (range: 63–95%) of species are threatened or driven to extinction when 50% or 90% of their habitat is lost. Additionally, the experts calculated that a 2°C or 5°C increase in global warming would drive approximately 25% (range: 15–40%) or 50% (range: 32–70%) of species to extinction [51]. Lichens are ubiquitous in terrestrial ecosystems across the globe and are ecologically significant symbioses that are well-known to non-scientists. They play an immense role in a variety of crucial ecological processes and ecosystem performance including as soil formation, nutrient cycling, rock weathering, and humidity regime regulation. The abundance and diversity of lichen across the globe have been declining. The main threats that apply to biodiversity in general are also true for lichens [39]. Lichens suffer from a loss of diversity and abundance on a variety of levels, ranging from entire communities to individual species and populations. The variety and abundance of lichens are adversely affected by numerous well-established human-mediated activities. Climate change and habitat loss are two of these challenges that affect almost all forms of biodiversity. Lichens are disproportionately affected by other hazards, such as air pollution, in comparison to other types of organisms. It has long been known that overbrowsing of the *Cladonia* by growing populations of reindeer in Scandinavia and Alaska is a major contributing element to the drastic loss in lichen cover, which could pose a significant threat to the husbandry of reindeer. The species richness and composition of lichen communities are significantly impacted by both deforestation and the deterioration of lichen habitats caused by the planting of plantation forests in place of natural forests [39].

Lichens are protected under the Endangered Species Act at the federal level in the USA. Currently, only two endemic species from the Southeast of the United States are listed as endangered species: *Cladonia perforata* and *Cetradonia linearis*. Since these species were added to the list more than 20 years ago, researchers have paid considerable attention to them, focusing mostly on mapping their ranges and learning about the genetics and demographics of the populations [22]. Effective lichen conservation plans typically integrate attempts to preserve or enhance the size, demographics, and genetic makeup of populations with the goal of protecting environments. The preservation of habitat size, connectivity, and quality should be the key goals of lichen conservation. In contrast to dynamic habitats like woods, grasslands, and gravel fields, permanent ecosystems like mountain ridges can best be preserved by static protection, which is also very simple to accomplish [39].

1.8 Conclusion

Lichens are the predominant flora on Earth exhibiting extensive biological, physiological, and chemical peculiarities. The fungal partner is the main component of the lichen thallus with regard to its morphology, but the algal partner is necessary from a nutritional standpoint. With the successful partnership of symbiosis, they are dominating a large terrestrial ecosystem on Earth. A wide range of secondary products has made them an essential natural treasure house for human food, medicine, and various industrial products.

They are useful organisms for ecosystem health monitoring. Various anthropogenic factors have made them threatened in natural habitats, especially some commercially used lichen species.

References

- 1 Armaleo, D., Müller, O., Lutzoni, F. et al. (2019). The lichen symbiosis re-viewed through the genomes of *Cladonia grayi* and its algal partner *Asterochloris glomerata*. *BMC Genomics* 20 (1): 605. <https://doi.org/10.1186/s12864-019-5629-x>.
- 2 Aprile, G.G., Catalano, I., Migliozi, A., and Mingo, A. (2011). Monitoring epiphytic lichen biodiversity to detect environmental quality and air pollution: the case study of Roccamonfina park (Campania Region - Italy). In: *Air Pollution—New Developments* (ed. A. Moldoveanu). InTech. <https://doi.org/10.5772/17907>.
- 3 Asplund, J. and Wardle, D.A. (2017). How lichens impact on terrestrial community and ecosystem properties. *Biological Reviews* 92 (3): 1720–1738. <https://doi.org/10.1111/brv.12305>.
- 4 Hawksworth, D.L. (1988). The variety of fungal-algal symbioses, their evolutionary significance, and the nature of lichens. *Botanical Journal of the Linnean Society* 96 (1): 3–20. <https://doi.org/10.1111/j.1095-8339.1988.tb00623.x>.
- 5 Saini, K.C., Nayaka, S., and Bast, F. (2019). Diversity of lichen photobionts: their coevolution and bioprospecting potential. In: *Microbial Diversity in Ecosystem Sustainability and Biotechnological Applications* (ed. T. Satyanarayana, S.K. Das, and B.N. Johri), 307–323. Singapore: Springer. https://doi.org/10.1007/978-981-13-8487-5_13.
- 6 Sanders, W.B. and Masumoto, H. (2021). Lichen algae: the photosynthetic partners in lichen symbioses. *The Lichenologist* 53 (5): 347–393. <https://doi.org/10.1017/S0024282921000335>.
- 7 Bhagarathi, L.K., DaSilva, P.N.B., Subramanian, G. et al. (2023). An integrative review of the biology and chemistry of lichens and their ecological, ethnopharmacological, pharmaceutical and therapeutic potential. *GSC Biological and Pharmaceutical Sciences* 23 (3): 092–119. <https://doi.org/10.30574/gscbps.2023.23.3.0223>.
- 8 Lutzoni, F. and Miadlikowska, J. (2009). Lichens. *Current Biology* 19 (13): R502–R503.
- 9 Zhao, Y., Wang, M., and Xu, B. (2021). A comprehensive review on secondary metabolites and health-promoting effects of edible lichen. *Journal of Functional Foods* 80: 104283. <https://doi.org/10.1016/j.jff.2020.104283>.
- 10 Aschenbrenner, I.A., Cernava, T., Berg, G., and Grube, M. (2016). Understanding microbial multi-species symbioses. *Frontiers in Microbiology* 7: 180. <https://doi.org/10.3389/fmicb.2016.00180>.
- 11 Duran-Nebreda, S. and Valverde, S. (2023). Composition, structure and robustness of lichen guilds. *Scientific Reports* 13 (1): 3295. <https://doi.org/10.1038/s41598-023-30357-w>.
- 12 Grube, M. (2018). The lichen thallus as a microbial habitat. *Biosystems Ecological Series* 34: 528–545.
- 13 Morillas, L., Roales, J., Cruz, C., and Munzi, S. (2022). Lichen as multipartner symbiotic relationships. *Encyclopedia* 2 (3): 1421–1431. <https://doi.org/10.3390/encyclopedia2030096>.

- 14 Leavitt, S.D. and Lumbsch, H.T. (2016). Ecological biogeography of lichen-forming fungi. In: *Environmental and Microbial Relationships* (ed. I.S. Druzhinina and C.P. Kubicek), 15–37. Springer International Publishing. https://doi.org/10.1007/978-3-319-29532-9_2.
- 15 Grimm, M., Grube, M., Schiefelbein, U. et al. (2021). The lichens' microbiota, still a mystery? *Frontiers in Microbiology* 12: 623839. <https://doi.org/10.3389/fmicb.2021.623839>.
- 16 Mitchell, M.E. (2007). Signposts to symbiosis: a review of early attempts to establish the constitution of lichen. *Huntia* 13 (2): 101–120.
- 17 Stanton, D.E., Ormond, A., Koch, N.M., and Colesie, C. (2023). Lichen ecophysiology in a changing climate. *American Journal of Botany* 110 (2): e16131. <https://doi.org/10.1002/ajb2.16131>.
- 18 Alexopoulos, C.J., Mims, C.W., and Blackwell, M. (2007). *Introductory Mycology*, 4e. Wiley.
- 19 Pichler, G., Muggia, L., Carniel, F.C. et al. (2023). How to build a lichen: from metabolite release to symbiotic interplay. *New Phytologist* 238 (4): 1362–1378. <https://doi.org/10.1111/nph.18780>.
- 20 Lichens (n.d.). Lichens of India. National Information Centre, Govt. of India. <https://bsi.gov.in/page/en/lichens>.
- 21 Payette, S. and Delwaide, A. (2018). Tamm review: the North-American lichen woodland. *Forest Ecology and Management* 417: 167–183. <https://doi.org/10.1016/j.foreco.2018.02.043>.
- 22 Allen, J.L., McMullin, R.T., Tripp, E.A., and Lendemer, J.C. (2019). Lichen conservation in North America: a review of current practices and research in Canada and the United States. *Biodiversity and Conservation* 28 (12): 3103–3138. <https://doi.org/10.1007/s10531-019-01827-3>.
- 23 Feuerer, T. and Hawksworth, D.L. (2007). Biodiversity of lichens, including a world-wide analysis of checklist data based on Takhtajan's floristic regions. *Biodiversity and Conservation* 16 (1): 85–98. <https://doi.org/10.1007/s10531-006-9142-6>.
- 24 Lakatos, M. (2011). Lichens and bryophytes: habitats and species. In: *Plant Desiccation Tolerance*, vol. 215 (ed. U. Lüttge, E. Beck, and D. Bartels), 65–87. Berlin Heidelberg: Springer. https://doi.org/10.1007/978-3-642-19106-0_5.
- 25 Molnár, K. and Farkas, E. (2010). Current results on biological activities of lichen secondary metabolites: a review. *Zeitschrift Für Naturforschung C* 65 (3–4): 157–173. <https://doi.org/10.1515/znc-2010-3-401>.
- 26 Lucking, R., Plata, E.R., Chavej, J.L. et al. (2009). How many tropical lichens are there. . . Really? *Bibliotheca Lichenologica* 100(Diversity of Lichenology –Jubilee Volume.): 399–418.
- 27 Singh, S., Arya, M., and Vishwakarma, S.K. (2019). Advancements in methods used for identification of lichens. *International Journal of Current Microbiology and Applied Sciences* 8 (08): 1450–1460. <https://doi.org/10.20546/ijcmas.2019.808.169>.
- 28 Büdel, B. and Scheidegger, C. (2008). Thallus morphology and anatomy. In: *Lichen Biology*, 2e (ed. T.H. Nash), 40–68. Cambridge University Press. <https://doi.org/10.1017/CBO9780511790478.005>.
- 29 Yang, J., Oh, S.-O., and Hur, J.-S. (2023). Lichen as bioindicators: assessing their response to heavy metal pollution in their native ecosystem. *Mycobiology* 51 (5): 343–353. <https://doi.org/10.1080/12298093.2023.2265144>.
- 30 Oksanen, I. (2006). Ecological and biotechnological aspects of lichens. *Applied Microbiology and Biotechnology* 73 (4): 723–734. <https://doi.org/10.1007/s00253-006-0611-3>.

- 31 Crawford, S.D. (2015). Lichens used in traditional medicine. In: *Lichen Secondary Metabolites* (ed. B. Ranković), 27–80. Springer International Publishing. https://doi.org/10.1007/978-3-319-13374-4_2.
- 32 Upreti, D.K., Divakar, P.K., and Nayaka, S. (2005). Commercial and ethnic use of lichens in India. *Economic Botany* 59 (3): 269–273. [https://doi.org/10.1663/0013-0001\(2005\)059\[0269:CAEUOL\]2.0.CO;2](https://doi.org/10.1663/0013-0001(2005)059[0269:CAEUOL]2.0.CO;2).
- 33 Devkota, S., Chaudhary, R.P., Werth, S., and Scheidegger, C. (2017). Indigenous knowledge and use of lichens by the lichenophilic communities of the Nepal Himalaya. *Journal of Ethnobiology and Ethnomedicine* 13 (1): 15. <https://doi.org/10.1186/s13002-017-0142-2>.
- 34 Pyakurel, D., Smith-Hall, C., Bhattarai-Sharma, I., and Ghimire, S.K. (2019). Trade and conservation of Nepalese medicinal plants, fungi, and lichen. *Economic Botany* 73 (4): 505–521. <https://doi.org/10.1007/s12231-019-09473-0>.
- 35 Yang, M.-X., Devkota, S., Wang, L.-S., and Scheidegger, C. (2021). Ethnolichenology—the use of lichens in the Himalayas and Southwestern Parts of China. *Diversity* 13 (7): 330. <https://doi.org/10.3390/d13070330>.
- 36 Llano, G.A. (1948). Economic uses of lichens. *Economic Botany* 2 (1): 15–45. <https://doi.org/10.1007/BF02907917>.
- 37 Sharma, M. and Mohammad, A. (2020). Lichens and lichenology: historical and economic prospects. In: *Lichen-Derived Products*, 1e (ed. M. Yusuf), 101–118. Wiley. <https://doi.org/10.1002/9781119593249.ch4>.
- 38 Wa, E., De, E.-G., and Gm, D. (2022). Lichens uses surprising uses of lichens that improve human life. *Journal of Biomedical Research & Environmental Sciences* 3 (2): 189–194. <https://doi.org/10.37871/jbres1420>.
- 39 Scheidegger, C. and Werth, S. (2009). Conservation strategies for lichens: insights from population biology. *Fungal Biology Reviews* 23 (3): 55–66. <https://doi.org/10.1016/j.fbr.2009.10.003>.
- 40 Galloway, D.J. (2008). Lichen biogeography. In: *Lichen Biology*, 2e (ed. T.H. Nash), 315–335. Cambridge University Press. <https://doi.org/10.1017/CBO9780511790478.017>.
- 41 Jahns, H.M. (1973). Anatomy, morphology, and development. *The Lichens* 3–58. <https://doi.org/10.1016/B978-0-12-044950-7.50006-4>.
- 42 Sanders, W.B. (2006). A feeling for the superorganism: expression of plant form in the lichen thallus. *Botanical Journal of the Linnean Society* 150 (1): 89–99. <https://doi.org/10.1111/j.1095-8339.2006.00497.x>.
- 43 Krishnamurthy, K.V. and Upreti, D.K. (2001). Reproductive biology of lichens. In: *Reproductive Biology of Plants* (ed. B.M. Johri and P.S. Srivastava), 127–147. Berlin Heidelberg: Springer. https://doi.org/10.1007/978-3-642-50133-3_7.
- 44 Bowler, P.A. and Rundel, P.W. (1975). Reproductive strategies in lichens. *Botanical Journal of the Linnean Society* 70 (4): 325–340. <https://doi.org/10.1111/j.1095-8339.1975.tb01653.x>.
- 45 Yamamoto, Y., Hara, K., Kawakami, H., and Komine, M. (2015). Lichen substances and their biological activities. In: *Recent Advances in Lichenology* (ed. D.K. Upreti, P.K. Divakar, V. Shukla, and R. Bajpai), 181–199. India: Springer. https://doi.org/10.1007/978-81-322-2235-4_10.
- 46 Culberson, C.F. and Elix, J.A. (1989). Lichen substances. In: *Methods in Plant Biochemistry*, vol. 1, 509–535. Elsevier. <https://doi.org/10.1016/B978-0-12-461011-8.50021-4>.

- 47 Podterob, A.P. (2008). Chemical composition of lichens and their medical applications. *Pharmaceutical Chemistry Journal* 42 (10): 582–588. <https://doi.org/10.1007/s11094-009-0183-5>.
- 48 Karunaratne, V. (1999). Lichen substances: biochemistry, ecological role and economic uses. *Ceylon Journal of Science: Physical Sciences* 6 (1): 13–28.
- 49 Poulsen-Silva, E., Gordillo-Fuenzalida, F., Atala, C. et al. (2023). Bioactive lichen secondary metabolites and their presence in species from Chile. *Metabolites* 13 (7): 805. <https://doi.org/10.3390/metabo13070805>.
- 50 Dasgupta, P. and Levin, S. (2023). Economic factors underlying biodiversity loss. *Philosophical Transactions of the Royal Society B: Biological Sciences* 378 (1881): 20220197. <https://doi.org/10.1098/rstb.2022.0197>.
- 51 Isbell, F., Balvanera, P., Mori, A.S. et al. (2023). Expert perspectives on global biodiversity loss and its drivers and impacts on people. *Frontiers in Ecology and the Environment* 21 (2): 94–103. <https://doi.org/10.1002/fee.2536>.