Chapter 6

Diversity, Ecogeography, and Importance of Lichens of Colombia

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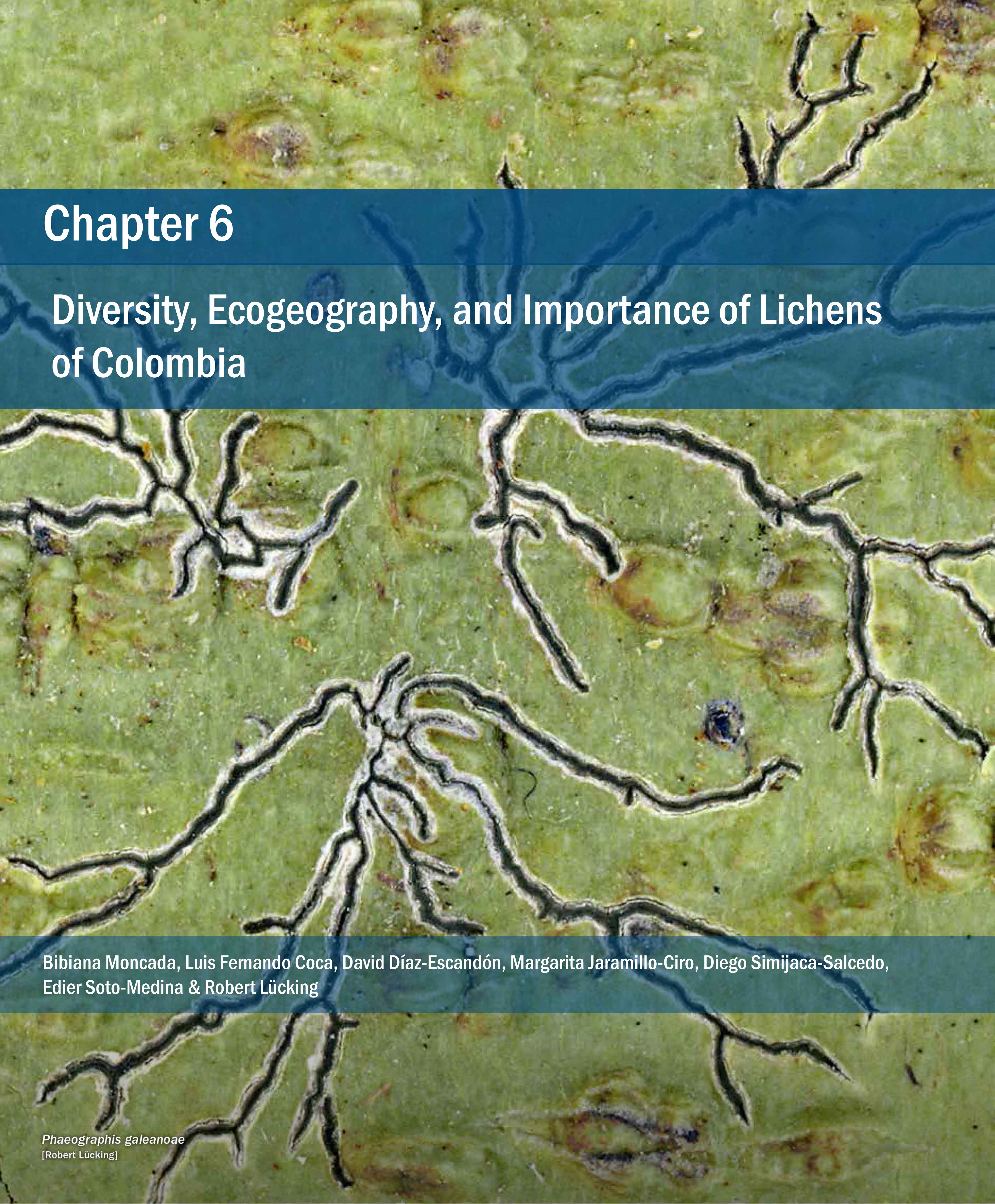

Phaeographis galeanoae
[Robert Lücking]

Chapter 6

Diversity, Ecogeography, and Importance of Lichens of Colombia

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ABSTRACT

Lichenised fungi constitute a substantial portion of the known Colombian fungi, with 2,670 out of 7,241 species. This fairly high number is not because lichens represent a particularly diverse group of fungi but because they are relatively well-studied in the country compared to non-lichenised fungi. Lichens have traditionally been defined as a symbiosis between a fungus (mycobiont), an alga and/or a cyanobacterium (photobionts). A modern definition also incorporates components of the lichen microbiome, particularly other fungi, and bacteria. However, the scientific names given to lichens strictly refer to the primary mycobiont. Globally, Colombia ranks among the top ten countries in terms of known lichen diversity. Most top-ranking countries are outside the tropics, so this supports Colombia's position among the three most biodiverse tropical countries worldwide. The total number for Colombia is estimated at 5,000 species, almost twice the number of species currently known. Unrecognised species are predicted to be found in understudied regions, understudied groups, and in genera where broad species concepts may include substantial hidden diversity. Diverse ecological studies assess environmental factors, such as altitudinal range, topography, and habitat diversity, as drivers of lichen biodiversity. On the basis of these findings, the impact of land-use changes and environmental pollution on lichen communities can be quantified, providing the foundation for using lichens as bioindicators to monitor ecosystem health and to perform environmental impact studies. However, such applications first require a systematic inventory of the lichens of Colombia.

RESUMEN

Los hongos liquenizados constituyen una parte sustancial de la funga Colombiana, con 2.670 de las 7.241 especies conocidas. Este número bastante alto no se debe a que los líquenes representen un grupo de hongos particularmente diverso, sino a que están relativamente bien estudiados en el país en comparación con los hongos no liquenizados. Los líquenes se han definido tradicionalmente como una simbiosis entre un hongo (micobionte) y un alga y/o una cianobacteria (fotobiontes). Una definición moderna también incorpora componentes del microbioma del liquen, en particular otros hongos y bacterias. Sin embargo, los nombres científicos dados a los líquenes se refieren estrictamente al micobionto primario. A nivel mundial, Colombia se encuentra entre los diez países con mayor diversidad de líquenes conocida. El pais de mayor diversidad liquénica conocido es Estados Unidos (4,341 especies), seguido por Brazil (4,310), Australia (4,003), China (3,050), Francia (2,917), México (2,722), India (2,714) e Italia (2,704). Sin embargo, la mayoría de los países con alta diversidad liquénica están fuera de los trópicos, lo que respalda la posición de Colombia entre los tres países tropicales con mayor biodiversidad en todo el mundo. El número total de especies liquenizadas para Colombia se estima en 5,000, casi el doble del número de especies conocidas actualmente. Se predice que las especies no reconocidas se encontrarán en regiones poco estudiadas, en grupos taxonómicos poco estudiados y en géneros donde los conceptos tradicionales de especies pueden incluir una alta diversidad críptica. Históricamente, Colombia es uno de los países más importantes en cuanto a estudios sobre líquenes neotropicales, junto a Brasil, Cuba y México. Los líquenes de Colombia se documentaron por primera vez como parte de la Expedición Botánica del Nuevo Reino de Granada y colecciones realizadas por Humboldt y Bonpland; sin embargo, las colecciones históricas de líquenes más importantes de Colombia son las de Lindig, en su mayoría estudiadas por Nylander. Consecuentemente, más de 400 tipos se encuentran en los herbarios H y PC, siendo una referencia histórica esencial para los líquenes (neo) tropicales. Diversos estudios ecológicos han evaluado los factores

ambientales, como el rango altitudinal, la topografía y la diversidad de hábitats, como impulsores de la biodiversidad de líquenes en Colombia. Con base en estos hallazgos, se puede cuantificar el impacto de los cambios en el uso de la tierra y la contaminación ambiental en las comunidades de líquenes, siendo la base para el uso de líquenes como bioindicadores para monitorear la salud de ecosistemas y realizar estudios de impacto ambiental. Sin embargo, tales aplicaciones requieren un inventario sistemático más profundo de líquenes de Colombia.

INTRODUCTION

Lichens have long been treated as a separate group of organisms, even after discovering their symbiotic nature (Lücking *et al.*, 2021). Biologically, lichens are just one example of the diverse nutritional types that have evolved among the *Fungi*, including saprotrophs, pathogens, mycorrhizas, and even carnivores (Watkinson *et al.*, 2016). However, in lichens, the vegetative hyphae form a persistent, macroscopically conspicuous thallus (Honegger, 2012; Figure 1). By contrast, non-lichenised fungi are characterised by ecologically hidden mycelia that are only usually visible due to their spore-bearing structures.

After its discovery, the lichen symbiosis has continuously been defined as bipartite or tripartite associations between a fungal partner (mycobiont) and one or two photosynthetic partners (photobionts; Lücking *et al.*, 2021). Known lichen mycobionts are only found in the two major phyla of the *Fungi*, representing either *Ascomycota* (99%) or *Basidiomycota* (1%) (Lücking *et al.*, 2017). At the same time, known photobionts encompass two domains and three kingdoms: *Chlorophyta* and *Heterokonta* among the eukaryotes and *Cyanobacteria* among the prokaryotes (Friedl & Büdel, 2008; Saini *et al.*, 2019). Recent studies using advanced molecular approaches have challenged the bipartite or tripartite nature of the lichen symbiosis, postulating that other fungi, in particular yeast-like *Basidiomycota*, as well as certain bacteria, together constitute the lichen microbiome as possible integral components of the lichen symbiosis (Grube *et al.*, 2015; Spribille *et al.*, 2016; Lendemer *et al.*, 2019; Hawksworth & Grube, 2020; Sierra *et al.*, 2020; Grimm *et al.*, 2021; Tuovinen *et al.*, 2021). Consequently, the definition of the lichen symbiosis as a bipartite or tripartite association of one mycobiont and one or two photobionts has been abandoned in favour of a broader definition encompassing these additional biological components (Hawksworth & Grube, 2020; Lücking *et al.*, 2021).

Owing to their symbiotic nature, the nomenclature applied to lichens has also posed challenges. Before discovery of the symbiosis, the scientific Latin name applied to the entire lichen, including its photobiont(s), at the time termed gonidia (Lücking *et al.*, 2021). With the realisation that lichens are composed of more than one organism, the need arose to adjust the precise application of the scientific name, which was then ruled to apply to the mycobiont alone (Lücking *et al.*, 2021). This solution seemed straightforward, but the argument could be raised that the same fungus may form different lichens, so-called photosymbiodemes, when associated with different photobionts (Figure 1), differing in ecology or distribution (Goward, 2008). The scientific name should be used for the mycobiont only to account for such cases, whereas the vernacular name can be used for the entire lichen. For example, in the case of the widespread *Xanthoria parietina* (yellow wall lichen), a species also found in Colombia, the scientific name (*X. parietina*) applies to the mycobiont alone. By contrast, the common name (yellow wall lichen) addresses the entire lichen (Lücking *et al.*, 2021).

Lichens are integral components of terrestrial ecosystems and sometimes are the dominant or exclusive life form (e.g., in the Antarctic continent). Even aquatic and marine lichens have been known for almost 50 years (Seaward, 1977; Sanders *et al.*, 2004; Feuerer & Hawksworth, 2007; Miądlikowska *et al.*, 2014). Lichens are generally believed to escape the temperate-tropical diversity gradient, being more conspicuous in temperate to arctic regions (Lücking *et al.*, 2011). However, this is a matter of scale: at larger scales (regional and landscape level), the species richness of temperate and tropical regions is comparable, whereas at smaller scales (local and habitat level), species richness appears to be greater in the tropics (Lücking *et al.*, 2011). Notably, the highest species richness is found in tropical lowland rainforests. Nonetheless, lichens are not conspicuous in these ecosystems, and their associated biomass is low. Yet, a single square kilometre (100 ha) of tropical rainforest can harbour up to 600 species, including several hundred species of foliicolous lichens growing on living leaves (Lücking *et al.*, 2011). For comparison, the best-studied temperate regions may yield higher species numbers, but across much larger areas, such as the Cévennes National Park in France (973 species within 93,700 ha), Glacier Bay National Park in Alaska (831 species within 600,000 ha), and Klondike Gold Rush National Historical Park (668 species within 5,300 ha), among others (Roux *et al.*, 2008; Spribille *et al.*, 2010, 2020; Lücking *et al.*, 2011). The main difference between these temperate and the hitherto studied tropical sites is that landscape diversity largely drives lichen diversity in the former. By contrast, high species richness has been reported in tropical locations for more or less homogeneous ecosystems, indicating that these habitats have a higher species carrying capacity (Lücking *et al.*, 2011).

BIODIVERSITY OF LICHENS OF COLOMBIA

Colombia is home to extraordinary biodiversity, given its geographic position at the conjunction between Central and South America. The country is bordered by two oceans, comprises an abrupt topography ranging from sea level to 5,775 m altitude, and has diverse ecosystems (Arbeláez-Cortés, 2013; Murcia *et al.*, 2013; Rangel-Ch., 2015). This great biodiversity also extends to lichens with 2,670 species reported to date from the country (Gaya *et al.*, 2021; this paper). Colombia is only surpassed in lichen richness by

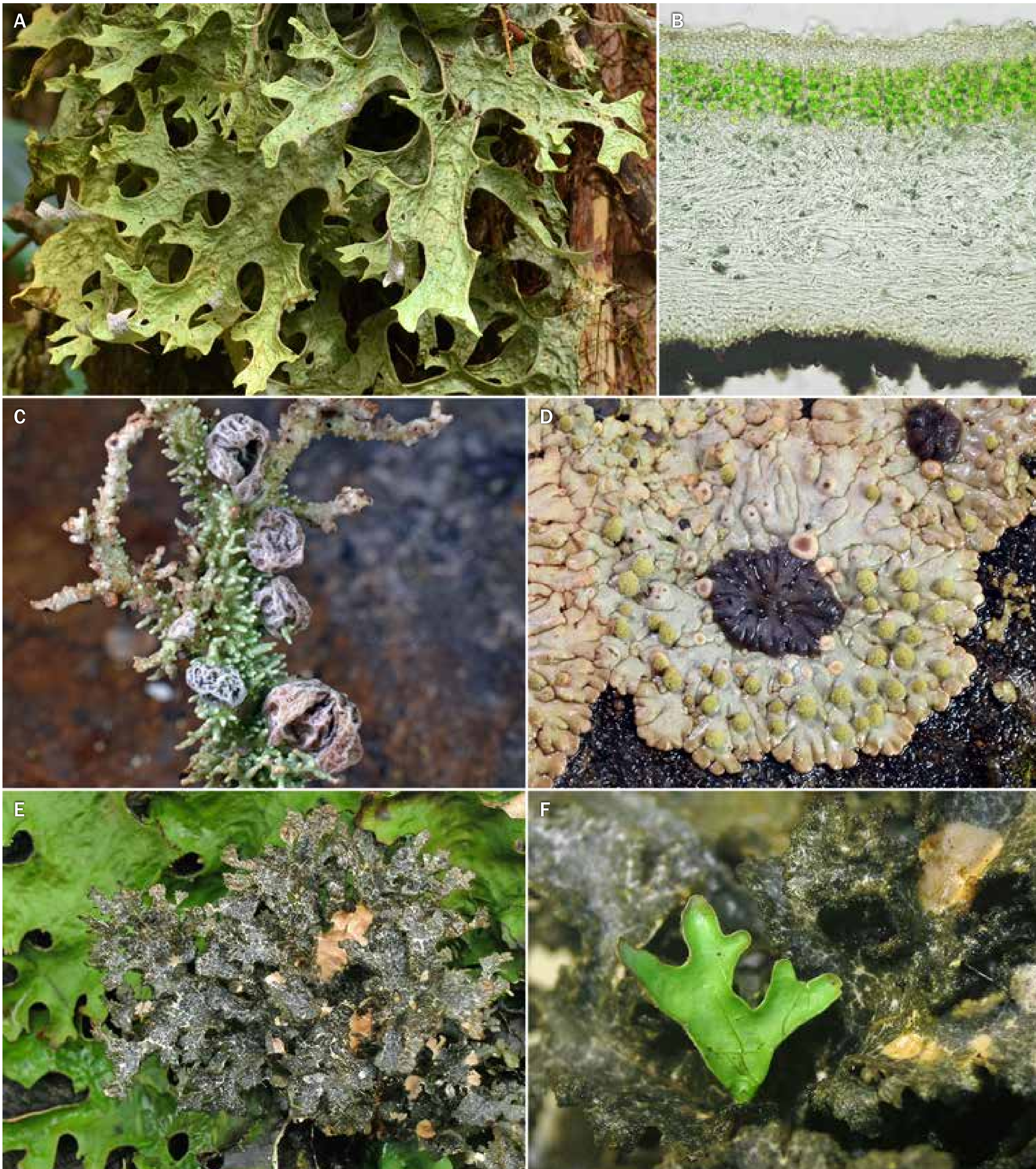

FIGURE 1. **A–B** Thallus of *Sticta lobarioides* and section of a Parmeliaceae showing the different layers formed by the mycobiont and the photobiont. **C–D** Cephalodia in *Stereocaulon novogranatense* (**C**) and *Placopsis rhodocarpa* (**D**). **E–F** Photosymbiodeme in *Sticta* aff. *subscrobiculata*, with cyanobacterial lobes emerging from green-algal lobes (**E**) and vice versa (**F**). (Photographs by Robert Lücking).

TABLE 1. Species numbers of lichenised fungi reported from selected regions and countries worldwide.

Country / territory	Number	Species / 1,000 km²	Species / $\log_2(km^2)$	Reference(s)
United States	4,341	0.44	187	Perlmutter & Weakley (2018); Esslinger (2019)
Brazil	4,310	0.51	187	Aptroot (2021)
Australia	4,003	0.52	175	McCarthy (2020)
China	3,050	0.32	131	Wei (2021)
France	2,917	4.53	151	Roux (2012)
Mexico	2,722	1.38	130	Herrera-Campos *et al.* (2014)
India	2,714	0.83	125	Singh & Sinha (2010); Sinha *et al.* (2018)
Italy	2,704	8.97	149	Nimis (2016)
Colombia	2,670	2.34	133	Gaya *et al.* (2021); this chapter
Austria	2,349	28.00	144	Hafellner & Türk (2016)
United Kingdom	2,000	8.25	112	Smith *et al.* (2009); Coppins (2021)
Germany	1,946	5.45	105	Wirth *et al.* (2011)
Japan	1,906	5.04	103	Ohmura & Kashiwadani (2018)
Chile	1,880	2.48	96	Galloway & Quilhot (1998); Vargas-Catillo & Sandoval-Leiva (2020)
Venezuela	1,801	1.97	91	Marcano *et al.* (1996); Hernández-M. (2021)
South Africa	1,751	1.44	87	Fryday (2015); Ahti *et al.* (2016)
Costa Rica	1,740	34.00	111	Umaña-Tenorio *et al.* (2002); Nelsen *et al.* (2006); Rivas Plata *et al.* (2006); Lücking *et al.* (2007, 2008); Aptroot *et al.* (2008); Sipman *et al.* (2012)
Argentina	1,670	0.60	78	Calvelo & Liberatore (2002)
Finland	1,644	4.86	90	Stenroos *et al.* (2016)
Bolivia	1,353	1.23	67	Rodriguez de Flakus *et al.* (2016)
Thailand	1,292	2.52	68	Buaruang *et al.* (2017)
Philippines	1,234	4.11	68	Paguirigan *et al.* (2020)
Algeria	1,051	0.44	50	Amrani *et al.* (2018)
Cuba	1,027	9.35	61	Lücking *et al.* (in prep.)
Peru	924	0.72	46	Ramos (2014)
Puerto Rico	781	85.79	59	Mercado-Díaz & Santiago-Valentin (2010)
Uruguay	614	3.48	35	Osorio (1972, 1992)
Madagascar	500	0.85	26	Aptroot (2016)
Panama	325	4.30	20	Piepenbring (2007)

FIGURE 2. A. Part of the “Lindig trail” in the “El Delirio Ecological Reserve”; **B** leading from the Southeastern outskirts of the municipality of Bogotá DC at 2,800 m altitude up to the paramo region of El Verjón at 3,400 m altitude, along the Río Fucha; **C** this area is the type locality for several species collected by Lindig, among them *Sticta peltigerella*, which typically grows on mossy boulders in streams and is an excellent indicator of water quality. (Photographs by Robert Lücking).

the USA (4,341 species), Brazil (4,310), Australia (4,003), China (3,050), France (2,917), Mexico (2,722), India (2,714), and Italy (2,704) (Singh & Sinha, 2010; Herrera-Campos *et al*., 2014; Nimis, 2016; Perlmutter & Weakley, 2018; Sinha *et al*., 2018; Esslinger, 2019; McCarthy, 2020; Aptroot, 2021; Wei, 2021; Table 1). These countries are much larger than Colombia (USA, Canada, Brazil, Australia, China, and India) or represent much better studied temperate countries (France and Italy). Among the ten richest countries in relative species density, Colombia ranks fourth with 2.34 species per 1,000 km^2, trailing Austria (28.0), Italy (8.97) and France (4.53), but ahead of Mexico (1.38), India (0.83), Brazil (0.52), Australia (0.52), the USA (0.44), and China (0.32). When considering a logarithmic relationship of species richness with area size, Colombia ranks seventh among the ten most species-rich countries [133 species per $\log_2$(area)], after the USA (187), Brazil (187), Australia (175), France (151), Italy (149), and Austria (144), but ahead of China (131), Mexico (130), and India (125). Some small countries or territories with comparatively high species numbers surpass the high species density of Italy, ranking far ahead of Colombia as well, such as Puerto Rico (85.8 species per 1,000 km^2), Costa Rica (34.0), and Cuba (9.4). Still, no further country included in this analysis has a higher species per $\log_2$(area) count than Colombia.

Overall, the high biodiversity of lichens of Colombia reflects that of other groups of organisms for the country, such as plants, vertebrates, and insects (see Chapter 3), and further supports the status of Colombia as one of the world's 17 megadiverse countries (Mittermeier, 1988; Mittermeier *et al*., 1999; Arbeláez-Cortés, 2013). It also corroborates Colombia's position as the second most biodiverse tropical country, after Brazil (Butler, 2016, 2019). Most other top-ranked countries and regions in terms of known lichen diversity are largely or entirely outside the tropics.

Historically, Colombia is one of the most important countries as regards studies on neotropical lichens, alongside Brazil, Cuba, and Mexico. Lichens of Colombia were first documented as part of the *Expedición Botánica del Nuevo Reino de Granada*, organised by José Celestino Mutis, with the collaboration of Francisco José de Caldas, between 1783 and 1816, with three colour plates representing the species *Baeomyces imbricatus* (≡ *Phyllobaeis imbricata*), *Cladonia didyma*, and *Stereocaulon ramulosum* (Aguirre-C., 1985; see Chapter 2). Halfway through this monumental endeavour, which unfortunately yielded few lichens and non-lichenised fungi, in 1801 Mutis and Caldas crossed pathways with Alexander von Humboldt and Aime Bonpland in Bogotá during the travels of the latter two through the northern Andes (Colombia, Ecuador, and Peru). The collections made by Humboldt and Bonpland were treated by Hooker (1822), who reported 73 species, including 12 presumably new to science, among them *Baeomyces imbricatus* (≡ *Phyllobaeis imbricata*), *Lecidea parmelioides* (= *Coccocarpia erythroxyli*), *Pyrenula marginata* (= *P. mamillana*), *Sticta humboldtii*, and *S. pallida* (≡ *Lobariella pallida*).

Alexander (Alexandre) Lindig, a German botanist who resided in Bogotá DC between 1859 and 1863, gathered Colombia's most important historical lichen collections (see Chapter 2). The famous "Lindig trail", presumably the type locality of many new species described from Bogotá DC, is still preserved in the "El Delirio" Reserve (Figure 2). Unfortunately, the exact localities of the collected specimens are unknown, as most only indicate "Bogotá". Most of Lindig's collections were studied in comprehensive treatments by Nylander (1859, 1863a–c, 1864, 1867). Over 400 types of names applying to (neo-) tropical species are now housed in the H and PC herbaria. This number is comparable to names based on type material from Cuba and only surpassed by the historical role of Brazil (Marcelli, 1998). Therefore, the Colombian lichen biota is an essential historical reference for (neo-)tropical lichens. In modern times, Harrie Sipman and collaborators (see Chapter 2) made substantial contributions to the knowledge of Colombian lichens, with comprehensive checklists enumerating 1,553 and more recently 1,674 species (Sipman *et al*., 2008; Sipman & Aguirre, 2016).

Although the currently known 2,670 species already represent a high number, the true diversity of the lichens of Colombia is probably much higher. Three reasons account for this assumption: 1. understudied and unexplored regions that harbour unknown species; 2. understudied taxonomic groups; and 3. refined species concepts in groups that were considered to be well-known. GBIF (https://www.gbif.org/occurrence/search?country=CO&taxon_key=180) has over 55,000 occurrence records for *Lecanoromycetes* in Colombia, which is by far the largest class of lichenised *Ascomycota*. Most of these records are georeferenced, but only 38% correspond to preserved specimens, whereas 62% represent human observations, mostly through environmental impact assessments. The resulting map shows a clear bias of existing collections to the Andean region. By contrast, the Caribbean, Pacific (Chocó biogeographic region), Orinoco, and Amazon regions are grossly undersampled (Figure 3). Such pattern is also seen for other organisms (Arbeláez-Cortés, 2013). Given that tropical lichens are particularly diverse at lower altitudes and dry forests often harbour unique taxa, many additional species can be expected from these four undersampled regions, which harbour large areas of lowland rainforests, savannas, and dry forests (Rincón-Espitia *et al*., 2011; Lücking *et al*., 2019; Soto-Medina *et al*., 2021). A particular hotspot is expected in the geographically isolated Sierra Nevada de Santa Marta, where only a few lichen studies have been carried out so far (Mägdefrau & Winkler, 1967; Nowak & Winkler, 1970; Sipman, 1986; Ramírez-Roncallo, 2018).

Understudied taxonomic groups are particularly represented by large genera that are either poorly collected or lack thorough taxonomic studies because they have been deemed too difficult to study. Two examples are the genera *Graphis* (and its recent segregate *Allographa*) and *Usnea*. In a revision of fungarium specimens, Motta & Amórtegui (2018) unveiled 15 new species and 67 new records of *Graphis* and *Allographa* for Colombia, some of which have been published (Motta *et al*., 2019), raising the number of species known from Colombia by 149%. A molecular

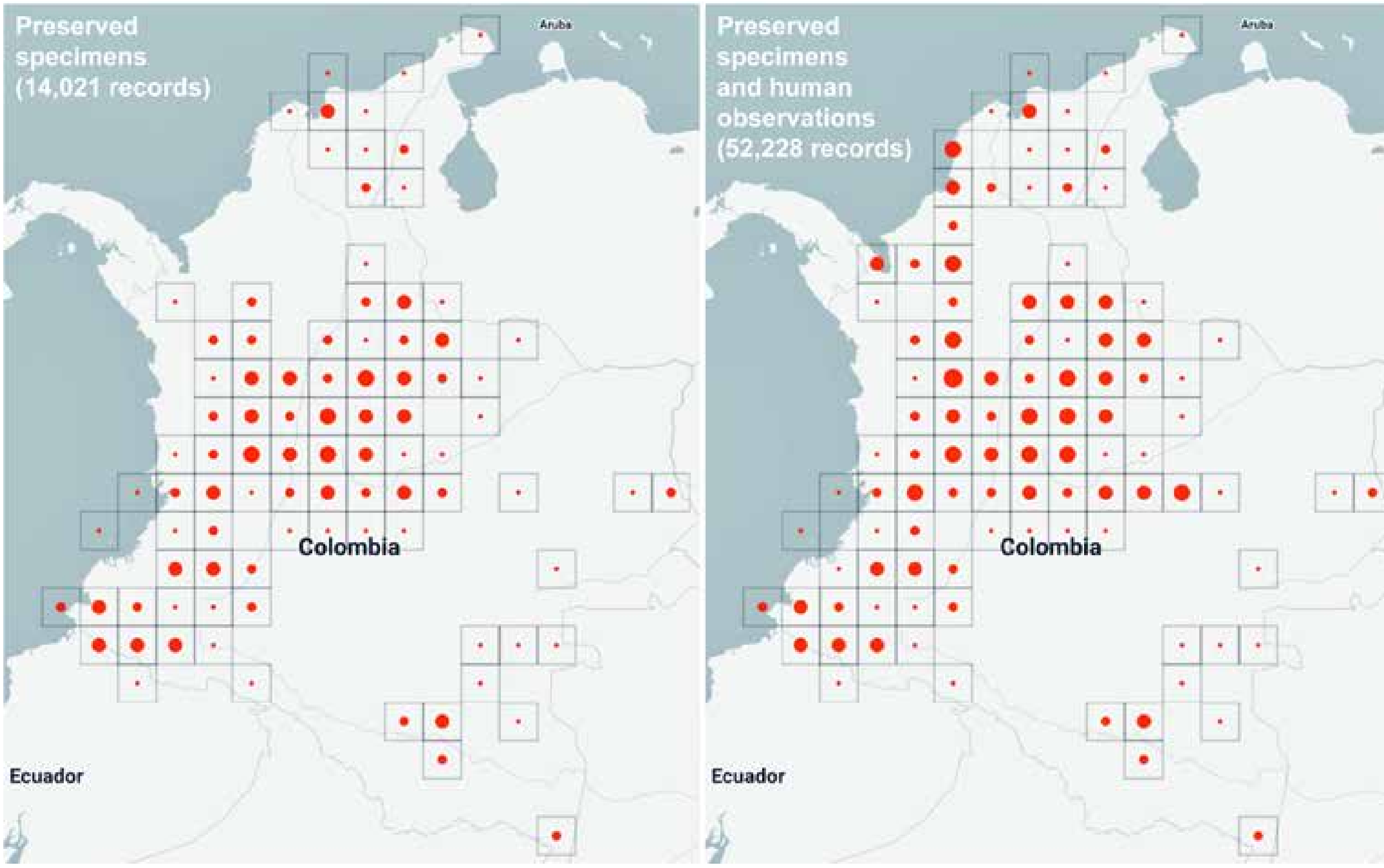

FIGURE. 3. Grid maps of georeferenced records of *Lecanoromycetes* in Colombia available from GBIF (https://www.gbif.org/occurrence/map?country=CO&taxon_key=180), showing records based on preserved specimens (left map) versus all records, i.e., also including human observations (right map). Size of dots is proportional to number of records per grid. Note that human observation records (mostly through environmental impact assessments) mitigate sampling gaps particularly in northwestern Colombia.

barcoding study of the genus *Usnea* suggested that its true species richness for Colombia may be up to 2.5 times greater than is currently known (Moncada *et al*., 2020). Some examples of refined species concepts are found in the genera *Lobariella* and *Sticta* (Ascomycota) and the genus *Cora* (Basidiomycota). Before molecular studies, the three genera were presumed to be well-known in Colombia, with four species of *Lobariella*, 42 of *Sticta*, and a single species of *Cora* (Sipman *et al*., 2008). Since then, these numbers have risen, based on molecular phylogenetic revisions, to 24, 78, and 49 species, respectively, increasing their species richness by more than 200%. This increase is particularly dramatic for the genus *Cora*, a well-known element of the Colombian Andean region.

Lücking *et al*. (2009) estimated the number of lichenised species in Colombia at 3,600. However, at that point, the magnitude of the hidden diversity in presumably well-known groups had not yet been realised. We anticipate that an estimated 3,600 species would perhaps cover additional species found in understudied regions or taxonomic groups. Yet, hidden diversity in presumably well-known lineages would on average double the number of species in many genera, adding another 1,500 species. Thus, a revised estimate, considering under- and unexplored regions, understudied groups, and hidden diversity would arrive at a number close to or above 5,000 species.

All major taxonomic groups and biotypes of lichens are represented in Colombia. However, compared to temperate lichen biotas, such as that of the United Kingdom, crustose groups are overrepresented, particularly those primarily confined to tropical regions, such as *Graphidales*, *Pyrenulales*, and *Trypetheliales*, which feature trentepohlioid photobionts adapted to tropical climates. By contrast, orders such as *Acarosporales*, *Baeomycetales*, *Lecideales*, *Pertusariales*, *Teloschistales*, and *Verrucariales*, are underrepresented (Figure 4). Additional orders, such as *Arthoniales*, *Caliciales*, *Lecanorales*, and *Peltigerales*, exhibit a similar richness in tropical and temperate regions but encompass different species. A particularly diverse group of tropical lichens are foliicolous taxa, which grow on the living leaves of vascular plants (Lücking, 2008; Mateus *et al*., 2012). The Colombian paramos is mentioned in terms

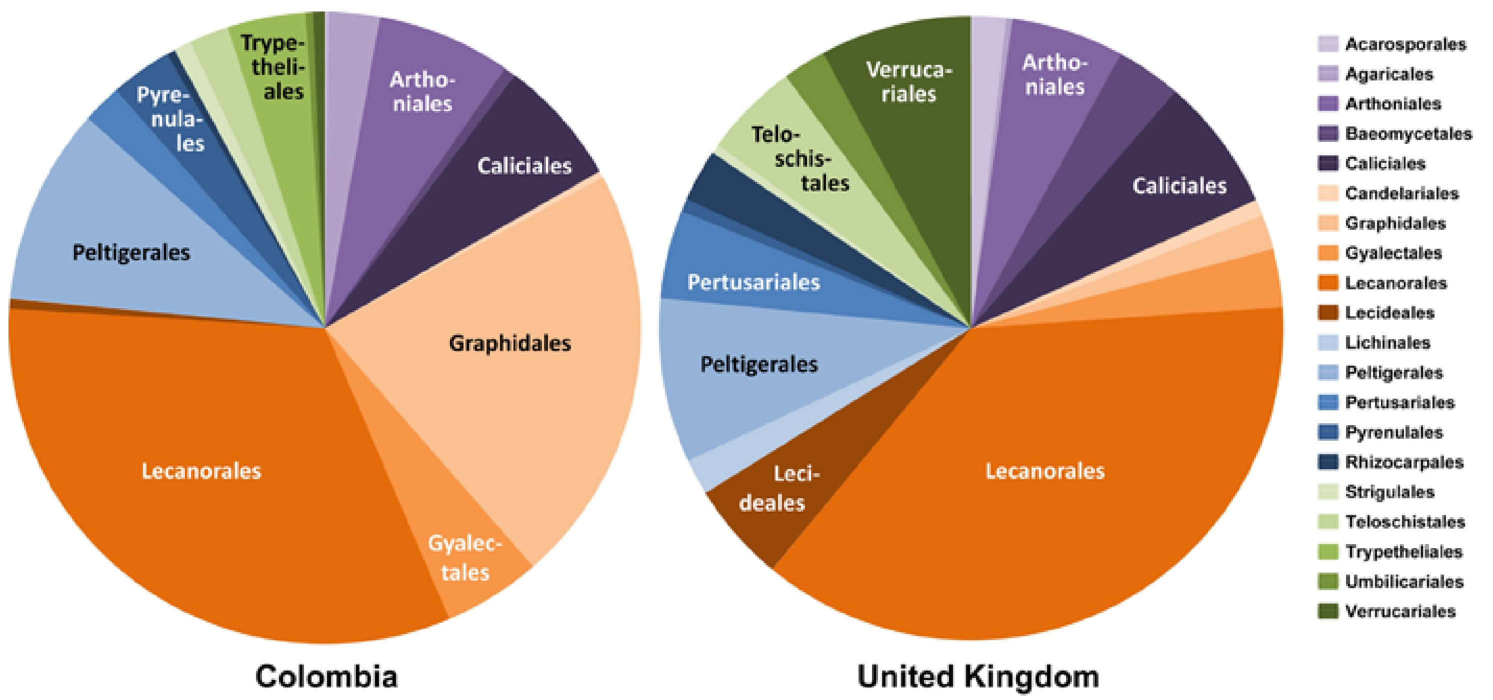

FIGURE 4. Comparison between Colombia and the United Kingdom in terms of the composition of lichenised fungi by order, representing a tropical versus temperate region. Data from Gaya *et al*. (2021) and this chapter for Colombia, and Smith *et al*. (2009) and Coppins (2021) for the UK.

of ecosystem diversity, featuring a high lichen biodiversity (Sipman, 2002; Cleef, 2008; Madriñán *et al*., 2013), with similar habitats only found in parts of Venezuela and northern Ecuador. By contrast, the lichen biota of the Colombian Amazon is broadly shared with neighbouring countries, such as Venezuela, the Guianas, Brazil, Ecuador, and Peru (Lücking *et al*., in prep.).

ECOGEOGRAPHY OF LICHENS OF COLOMBIA

Compared to temperate regions in North America and Europe, studies on the ecology and distribution of Colombian lichens are still sparse. Regarding the distribution patterns of Colombian lichens, to date, there is no quantitative analysis, so here we provide a first approach based on the assessment of 2,678 species (Figure 5). According to this assessment, most species (35%) are neotropical, followed by subcosmopolitan (16%), circumpacific (15%), and pantropical (15%) species. Only a small portion of 8.5% is currently considered endemic. However, this assessment is preliminary, as molecular studies have shown that presumably widespread taxa often represent species complexes. Thus, we expect the actual proportion of widespread, cross-continental species to be lower, favouring a higher number of neotropical and endemic taxa (see Chapter 10). Furthermore, species currently classified as circumpacific (i.e., known from the Neotropics and the Eastern Paleotropics) are largely artefactual due to a lack of data from tropical Africa where these species may occur.

The division of Colombia into ecoregions (IDEAM *et al*., 2017) provides an excellent background for investigating tropical lichens beyond their taxonomy and systematics. Ecological, ecogeographical, and biogeographical studies of Colombian lichens go back to the early 1970s, covering topics such as distribution patterns, landscape ecology, altitudinal gradients, and habitat preferences (Sipman, 1986, 1989, 1998; Ahti, 1992; Wolf, 1993a; Kessler, 2000; Aguirre-C. & Sipman, 2004; Pinzón & Linares, 2006; Aguirre-C., 2008; Aguirre-C. & Rangel-Ch, 2008; Pérez-Quintero & Watteijne-Cerón, 2009; Moncada *et al*., 2014). Other studies focused on community and population structure, substrate specificity, and niche differentiation (Nowak & Winkler, 1970, 1975; Wolf, 1993b, c, 1994, 1995; Soto-Medina *et al*., 2012, 2015; Zárate-Arias *et al*., 2019). More recent studies have investigated functional traits of tropical lichens (Chilito-López *et al*., 2016; Soto-Medina *et al*., 2019) or their ecophysiology (Pulido-Herrera & Ramos-Montaño, 2016), whereas some classic studies analysed lichen-related nitrogen availability and nutrient flux in tropical forest ecosystems (Forman, 1975; Veneklaas, 1991). Interactions between lichens and invertebrates, specifically regarding lichen-related camouflage, are a popular topic in entomological studies (Rivera *et al*., 2011; Cadena-Castañeda, 2013; Londoño *et al*., 2017; Lisi *et al*., 2019). The availability of advanced molecular methods in Colombian laboratories has also allowed new investigations into the microbiome of paramo lichens, revealing patterns of host specificity (Sierra *et al*., 2020). Additionally, several studies have addressed the impact of land use change on lichen community diversity and composition (Ardila-Rios *et al*., 2015; Pulido-Herrera & Ramos-Montaño, 2016; Ramírez-Morán *et al*., 2016; Simijaca *et al*., 2018).

Colombia served as the target region for one of the most important broad-scale ecological studies on tropical ecosystems, the ECOANDES project (Van der Hammen *et al*., 1983). ECOANDES was an extraordinary example of collaborative work between Colombian and Dutch researchers during the early 1980s (see Chapter 2), leaving a lasting impact in the development of Colombian biodiversity research and resulting in various studies on lichenised fungi (Sipman, 1986, 1989, 1998; Kessler, 2000; Aguirre-C., 2008). The study area encompassed all four major mountain systems of Colombia: the Sierra Nevada de Santa Marta, the Western Cordillera (Tatamá), the Central Cordillera (Los Nevados), and the Eastern Cordillera (Sumapaz). Besides more inventory-oriented lichen studies, the ECOANDES project also produced the seminal dissertation by Jan Wolf on epiphytic canopy communities on Colombian montane forests, including numerous new data on lichens (Wolf, 1993a-c, 1994, 1995). Starting with the ECOANDES project, Harrie Sipman became a pioneer in modern lichen research in Colombia and a mentor of Jaime Aguirre-Ceballos, who continued the studies on the ecogeography of Colombian lichens (Aguirre-C. & Rangel, 2008).

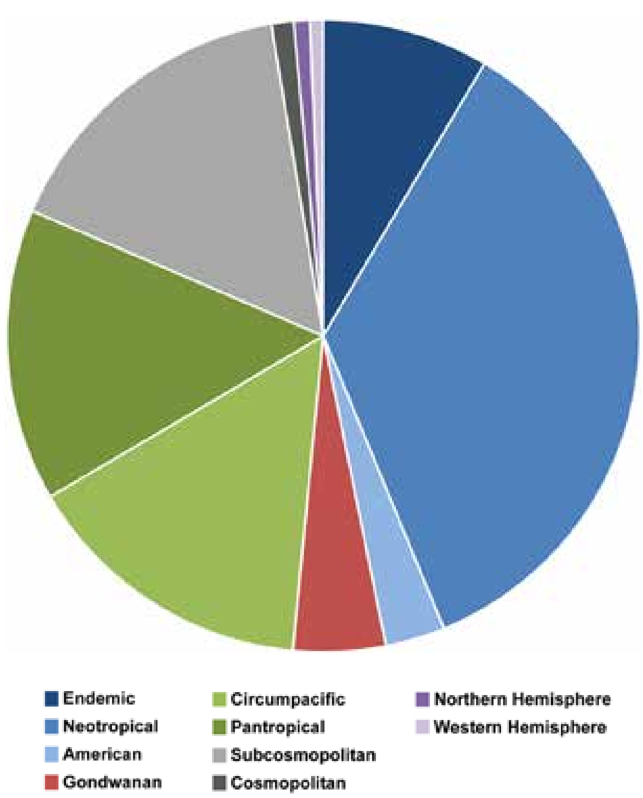

FIGURE 5. Main distribution types among the 2,678 species of lichenised fungi known from Colombia.

These diverse studies have provided insight into which environmental factors drive lichen biodiversity and species richness, demonstrating how the diversity and composition of lichen communities depend on macroecological features driven by altitude and other factors. Moncada *et al*. (2014) demonstrated that (sub-)Andean Forests and Páramo areas harbour the highest richness of *Sticta* species, with the Eastern Cordillera as one of the centres of diversity for the genus. Soto-Medina *et al*. (2012) found subtle phorophyte preferences of lichens, with a stronger dependency on microclimatic factors. Chilito-López *et al*. (2016) also found pronounced microhabitat preferences among lichenised taxa correlated with functional parameters, such as growth form. Unfortunately, a comprehensive database in terms of functional parameters does not yet exist for the lichens of Colombia or tropical lichens in general, but this would be a desirable achievement for the near future to allow more thorough assessments in trait-based functional ecosystem analyses (St. Martin & Mallik 2017).

Impact studies suggest that the replacement of natural forests with tree monocultures natural forests influence influences lichen communities. Thus, *Eucalyptus* plantations in Colombian montane *Quercus* forests have a strong dediversification and homogenisation effect, with planted trees featuring highly similar lichen communities, leading to low plot-level species richness (Ardila-Rios *et al*., 2015). Notably, replacing native *Quercus* forests with *Pinus* plantations does not seem to affect diversity metrics but causes partial species turnover (Simijaca *et al*., 2018). Pulido-Herrera & Ramos-Montaño (2016) found a marked edge effect on lichen community parameters and chlorophyll content in fragments of *Polylepis* forests in the páramo zone, and Ramírez-Morán *et al*. (2016) associated functional biotypes with the conservation status of Andean Forest remnants.

IMPORTANCE OF LICHENS OF COLOMBIA

Lichens are important components of tropical ecosystems, developing conspicuous biomass particularly in montane forests and paramos, but high diversity, especially in lowland to lower montane rainforests (Sipman & Harris, 1989; Lücking *et al*., 2011). Their ecosystem services encompass the water and nutrient cycle, generating local humidity and cloud cover, preventing soil erosion, and contributing to atmospheric nitrogen fixation (Seaward, 1988; Ahmadjian, 1995; Zedda & Rambold, 2015), as well as diverse interactions with animals,by supporting nest building or camouflage (Seaward, 1988).

As symbiotic organisms, lichens have adapted to diverse conditions that may be averse to other organisms. However, they are susceptible to abrupt environmental changes, particularly air pollution, habitat disturbances, and land-use change. Therefore, they have long been used as bioindicators of environmental health. In Colombia, since 1977, more than 20 theses have been focused on lichens as pollution indicators in different areas of the country. The first published studies were those of Rubiano-Olaya (1987, 1988) in Cali and Medellín. From the beginning, most of these studies were based on lichen community ecology parameters, employing the *Index of Atmospheric Purity* (IAP), which links the frequency and abundance of individual taxa to sample species composition, providing a taxon-independent measure for air quality. The IAP was also used to determine isocontamination zones in various areas of Bogotá DC (Rubiano-Olaya, 2002; Rubiano-Olaya & Chaparro, 2006; González-Aldana, 2007), Tunja (Simijaca-Salcedo *et al*., 2011, 2014), and Quibdó (Mena, 2012), particularly in relation to vehicular traffic (Valois-Cuesta & Mosquera-Palacios, 2014). In Medellín, an updated study confirmed the usefulness of the IAP across a broader range of phorophytes, using air quality monitoring stations as reference (Correa-Ochoa *et al*., 2020), and the method was also employed to assess air quality in suburban areas near Medellín (Quijano-Abril *et al*., 2021). While broadly comparable between regions, the downside of the IAP method is that it does not require complete identification of the underlying lichens, as long as they are accurately recognised as species. Therefore, most of the studies mentioned above do not provide complete lists of fully identified species, making a proper taxonomic assessment of urban lichen diversity difficult to obtain. In addition to biomonitoring using the IAP, a few studies in Colombia have assessed the impact of atmospheric pollutants, including emissions in a sulphur mine in Cauca (Diaz-Escandón *et al*., 2016), acid rain (Álvarez-Berrio *et al*., 2018), and heavy metals in lichens from Bogotá DC (Rodriguez *et al*., 2016).

The potential application of lichens to monitor the impact of land use changes are thus far from limited to montane forest ecosystems (Ardila-Rios *et al*., 2015; Diaz-Escandón *et al*., 2016; Pulido-Herrera & Ramos-Montaño, 2016; Ramírez-Morán *et al*., 2016; Simijaca-Salcedo *et al*., 2018). Unfortunately, standardised protocols for this purpose are not yet available. Ramírez-Morán *et al*. (2016) assessed the strategy of using easy-to-identify lichen biotypes instead of actual lichen taxa, providing an advantage like that of the IAP. In Colombia, lichens, mosses, and vascular epiphytes have been traditionally protected under the *Resolución 213 de 2013* of the Ministerio de Ambiente y Desarollo Sostenible (MinAmbiente), initially aiming to prevent the uncontrolled harvesting and trade of these organisms. For the past decade, this provision has been implemented to monitor the environmental impact of projects related to infrastructure or the exploration of mineral resources. Unfortunately, this approach bears a few problems: sampling protocols are not standardised, the underlying taxonomy is often inaccurate, and there are conflicts of interest if the entity that carries out the project is also responsible for the impact report. A solution could be a standardised protocol using selected lichen taxa that are known to be sensitive to environmental changes, such as thelotremoid Graphidaceae or lobarioid Peltigeraceae (Rivas Plata *et al*., 2008; Ramírez-Morán *et al*., 2016), combined with an assessment of the conservation status of the underlying ecosystem (Etter *et al*., 2018).

Another venue in terms of lichen uses is the diverse composition of secondary substances and their potential applications (Mitrović *et al*., 2011). Some studies on this topic have been performed in Colombia (Perico-Franco *et al*., 2015; Valencia-Islas *et al*., 2020). Unfortunately, most studies do not go beyond reporting the results from standardised bioassays, and potential clinical applications are rarely explored (Lücking, 2020). The causes of antibacterial, antitumoral or antioxidative effects are often unclear, because the bioactive compounds are not always identified, or substances are tested separately, without considering potential interactions with other substances. Another issue is inaccurate taxonomy, as experts are rarely consulted, and the underlying material is often not documented by proper voucher material. Fortunately, the aforementioned Colombian studies are exemplary in this respect, as they cited voucher material and consulted taxonomic experts.

Although promising, applied approaches using lichens depend on accurate assessment of the underlying biodiversity and hence require rigorous taxonomic studies and inventories using modern methods, including molecular assessments. Therefore, the political support for science should not focus on applied aspects alone but should also provide the framework for the necessary taxonomic inventories.

CONCLUSIONS

The currently known number of 2,678 species makes the Colombian lichen funga one of the richest worldwide. However, the actual number may be almost twice as high, requiring further rigorous inventory works and taxonomic revisions, particularly in the understudied regions of the Caribe, Orinoquía, Pacífico and Amazonía. Unfortunately, societal and government support for such fundamental studies in Colombia is limited. Instead, there is a strong focus on applied aspects, including in the training of young students, neglecting the knowledge and tools that are necessary to properly assess the underlying taxonomy. Before undertaking applied studies, efforts should concentrate on providing a complete inventory of the Colombian lichen biota so that potential applications can be assessed and explored more rigorously, taking into account the need for habitat conservation to preserve this diversity. In applied studies, the focus should be on broadly applicable, standardised approaches, such as using lichens as biomonitors of air pollution and environmental health. Pharmaceutically oriented studies should be more systematically structured to provide new insight into the potential of lichen secondary metabolites, seeking collaborations for follow-up clinical studies when results are promising.

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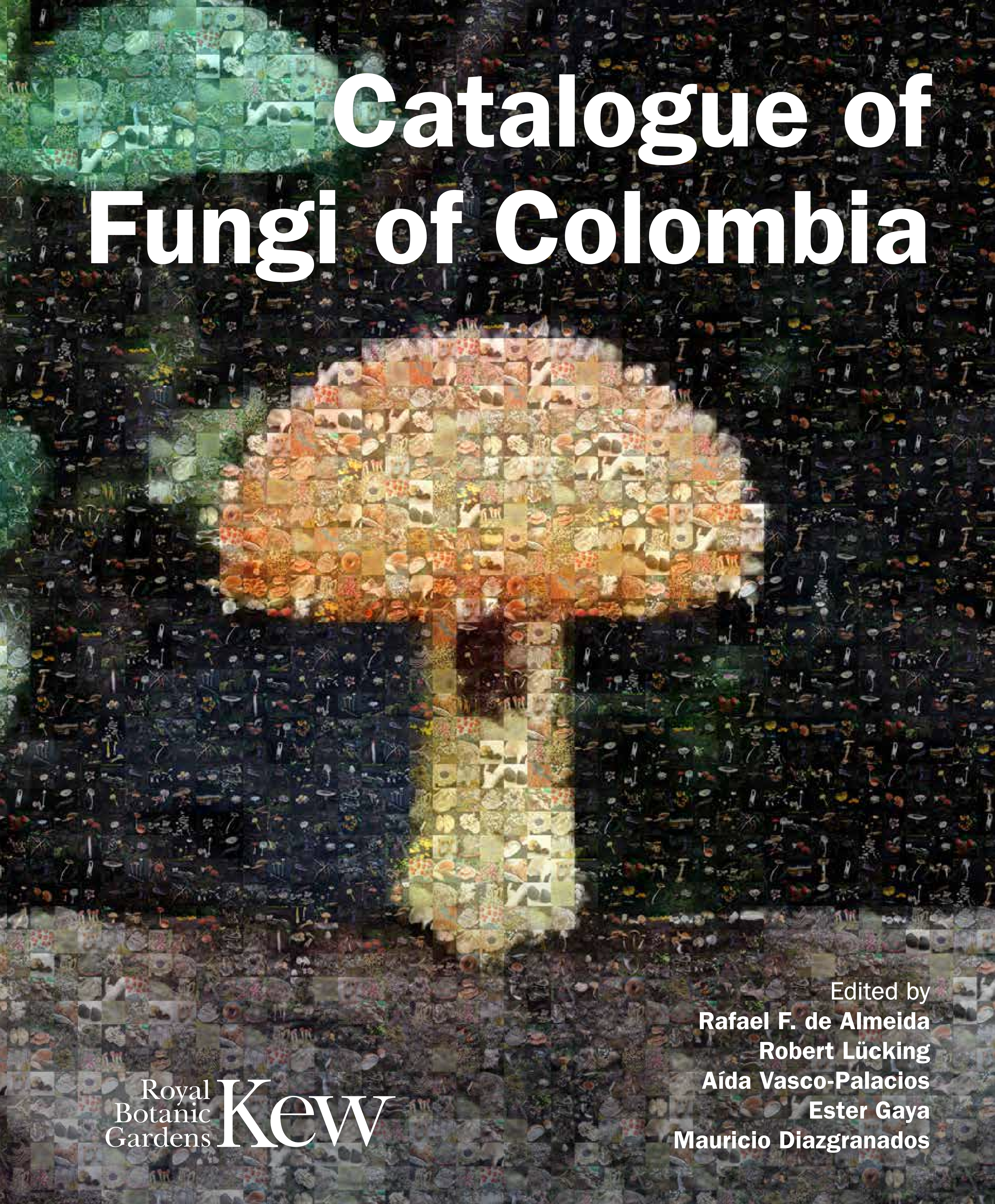
Enchylium conglomeratum
[Robert Lücking]



Catalogue of Fungi of Colombia

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The *Catalogue of Fungi of Colombia* is the first comprehensive listing of the known Colombian funga. Compiled by a team of Colombian and international mycologists from the Royal Botanic Gardens, Kew, the Humboldt Institute and numerous partner institutions, it consolidates expert-generated information linked and accessible through an online portal (Col*Fungi*). The checklist is accompanied by 15 chapters written by specialists, providing perspectives on the state of knowledge on the Colombian funga, covering a range of topics, from the diversity of the main groups of fungi and the history of mycological studies in this country, to aspects of the biogeography, ecology, biotechnology, conservation, and uses of Colombian fungi and their presence in national and international biological collections. The Catalogue is further enriched by diverse supplementary material, allowing users to explore further open questions and opportunities, to develop new ideas on the use of fungi and their conservation, and to foster social and environmental awareness.

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