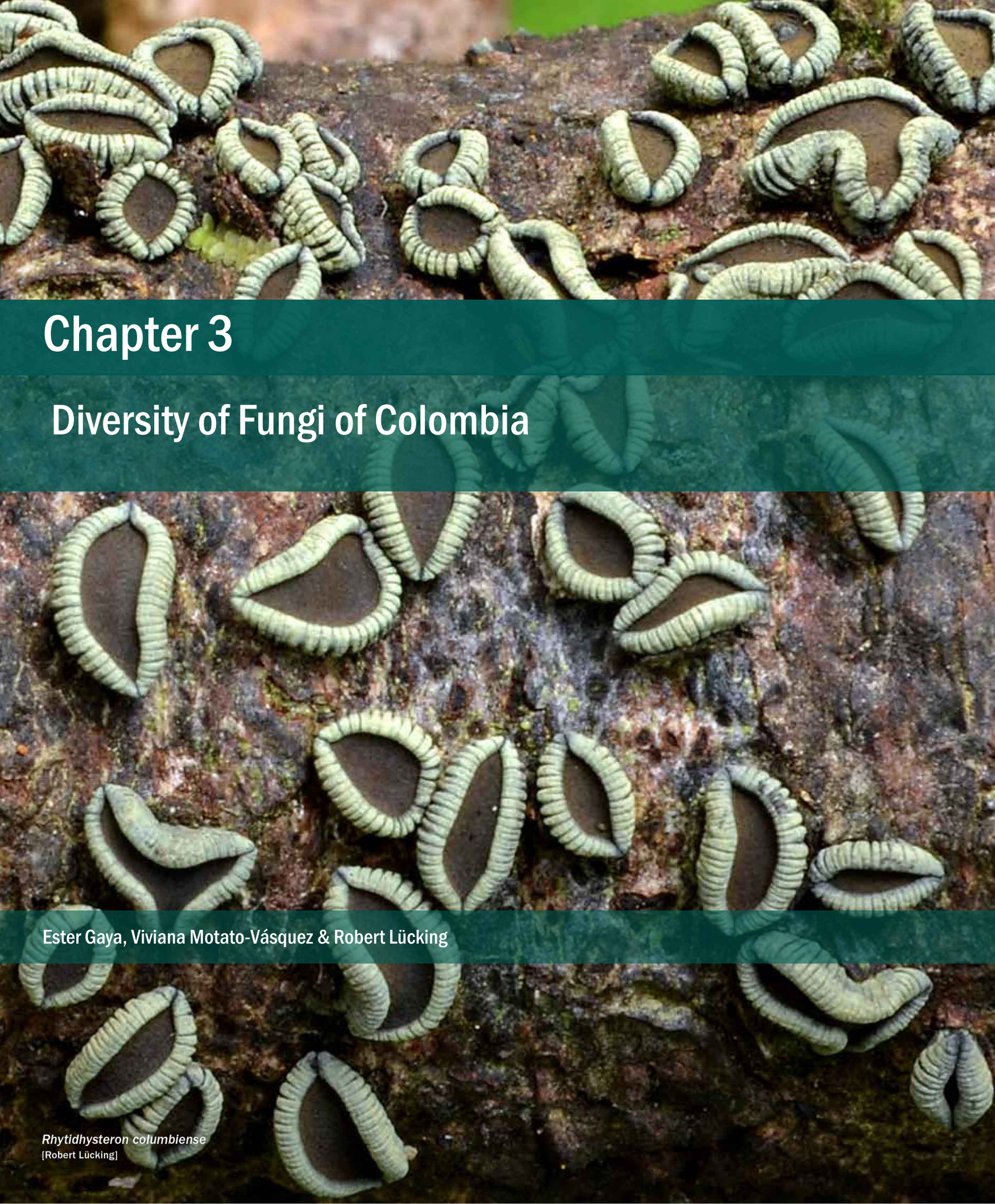

Chapter 3

Diversity of Fungi of Colombia

Ester Gaya, Viviana Motato-Vásquez & Robert Lücking

Rhytidhysteron columbiense
[Robert Lücking]

Chapter 3

Diversity of Fungi of Colombia

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Keywords: animals, Colombian biodiversity, insects, global estimate, plants.

ABSTRACT

This chapter provides a brief overview of the diversity of fungi of Colombia, both in comparison with other organisms and in a global context, including an assessment of the current state of knowledge and an estimate of the actual species richness. The current checklist of fungi of Colombia, including lichenised and fungus-like organisms unrelated to the true *Fungi*, comprises 7,241 species. Assessments of biodiversity-rich countries are usually based on plants and vertebrates, but here we provide an expanded perspective, including fungi and selected invertebrates. The documented diversity of fungi of Colombia is lower than that of plants, vertebrates, and insects, which we attribute to the lack of rigorous taxonomic studies and systematic inventories. Colombia ranks second in plant and vertebrate diversity in the world, trailing only Brazil. However, in terms of known fungal diversity, Colombia is not among the top ten countries and even far behind smaller temperate countries, such as France, Italy, the UK, Germany, and Japan, again highlighting the need for much additional work. Estimates of the existing species richness of fungi of Colombia oscillate between 27,430 and 380,000 species, depending on the extrapolation method. Although these numbers may seem exaggerated, currently reported numbers for the United States already exceed 45,000 and estimates for Mexico predict up to 260,000 species. To catalogue the diversity of the Colombian funga fully, a thorough assessment is needed, including molecular studies of presumably known taxa that may include morphologically cryptic species and effective detection methods for ecologically hidden fungi.

RESUMEN

Este capítulo proporciona una breve introducción a la diversidad de hongos de colombia, tanto en comparación con otros organismos como en un contexto global, incluyendo una evaluación del estado actual del conocimiento y una estimación de la riqueza real de las especies. El listado actual de los hongos de colombia comprende 7.241 especies, incluyendo especies liquenizadas y organismos similares a los hongos pero no relacionados con los hongos verdaderos, tales como los oomicetes y los mixomicetes. Si bien las evaluaciones de los países ricos en biodiversidad generalmente se basan en plantas y vertebrados, aquí brindamos una perspectiva ampliada, la cual incluye los hongos e también invertebrados seleccionados. La diversidad documentada de hongos de colombia es menor que la de plantas (26,150 especies), vertebrados (7,607) e insectos (68,000), lo que atribuimos a la falta de estudios taxonómicos rigurosos e inventarios sistemáticos. Colombia ocupa el segundo lugar en diversidad de plantas y vertebrados en el mundo, solo detrás de Brasil. Sin embargo, en términos de diversidad fúngica conocida, Colombia no se encuentra entre los diez primeros países del mundo e incluso muy por detrás de algunos países templados más pequeños, como Francia (24,840 especies), Italia (22,700), el Reino Unido (20,000), Alemania (15,295) y Japón (14,000), lo que también destaca la necesidad de mucho trabajo adicional. Las estimaciones de la riqueza de especies existentes de hongos de colombia oscilan entre 27,430 y 380,000 especies, según el método de extrapolación. Si bien estos números pueden parecer exagerados, los números reportados actualmente para los Estados Unidos ya superan las 45,000 y las estimaciones para México predicen hasta 260,000 especies. Para catalogar completamente la diversidad de los hongos de colombia, se necesita inventarios exhaustivos, los cuales incluyen estudios moleculares de taxones supuestamente conocidos que pueden incluir especies morfológicamente crípticas, tanto como métodos efectivos de detección de hongos ecológicamente escondidos, a travez del metabarcoding ambiental.

INTRODUCTION

Fungi represent one of the three major eukaryotic life forms on our planet, besides plants and animals (Burki *et al*., 2019). Mycology, the study of fungi, was traditionally treated as a branch of botany, but fungi are more closely related to animals than plants (Figure 1). To further complicate matters, fungi are not a natural group, with fungal life forms convergently evolving several times among eukaryotes. We can even find fungus-like bacteria in the Actinomycetales (Ventura *et al*., 2007). Although nearly 99% of all fungi are representatives of the kingdom *Fungi*, fungus-like organisms are also found in various other clades (Beakes & Thines, 2017; Burki *et al*., 2019; James *et al*., 2020). These include the *Oomycota* (egg fungi or water moulds), *Hyphochytridiomycota*, and *Labyrinthulomycetes* (slime nets), which form separate lineages within the *Heterokontophyta* (part of the SAR supergroup and related to brown algae and diatoms), as well as the *Phytomyxea* within the *Rhizaria* (also part of the SAR supergroup). Other fungus-like organisms are represented by the *Myxogastria* or *Myxomycetes* (plasmodial slime moulds) within the *Amoebozoa*, the *Acrasida* (cellular slime moulds) within the *Discoba*, and the *Fonticulida* (another group of cellular slime moulds) within the *Cristidiscoidea*, a clade basally related to the *Fungi* and together with the

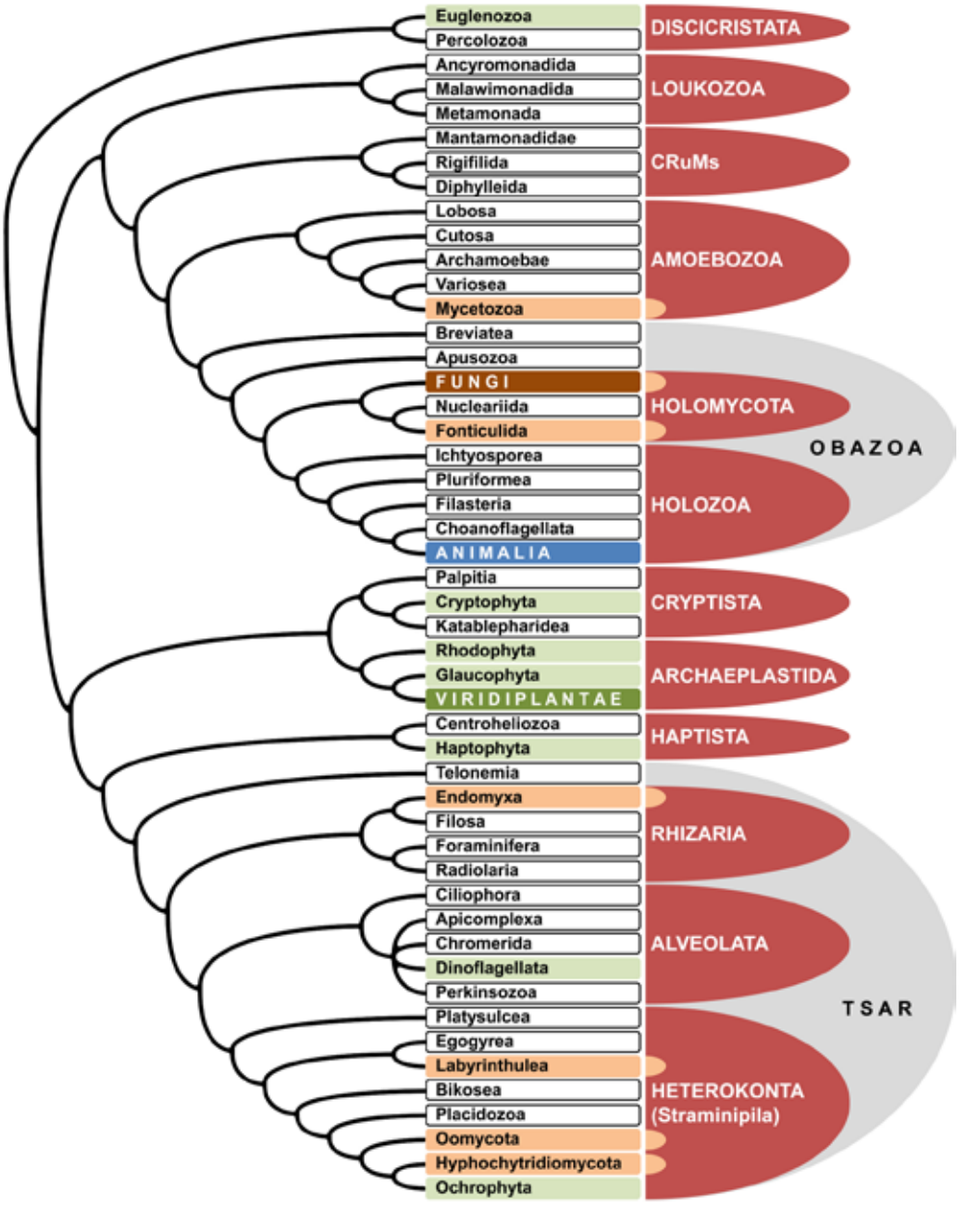

FIGURE 1. Simplified *Tree of Life* highlighting the position of the true *Fungi* (dark brown) and other fungus-like organisms (light brown) relative to animals (*Animalia*) (blue) and true plants (*Viridiplantae*) (dark green) and plant-like organisms (light green) (compiled after Burki *et al*., 2019 and James *et al*., 2020, as well as various other sources for specific clades). Unranked major groups above kingdom are indicated to the right.

latter forming the *Holomycota* (Figure 1). The true fungi are named *Fungi* (as a scientific name written in upper case and italics) to distinguish them from other fungus-like organisms, whereas the non-scientific term "fungi" also encompasses all unrelated fungus-like organisms (as a vernacular name written in lower case and standard font; Thines *et al*., 2020).

The convergent evolution of the fungal lifestyle within the eukaryotes is comparable to the situation in plants (Burki *et al*., 2019; James *et al*., 2020): the true plants are grouped in the kingdom *Plantae* (corresponding to the unranked *Viridiplantae*), but other multicellular plant-like organisms are found in the related red (*Rhodophyta*) and brown algae (Phaeophyceae), the latter classified within the *Heterokontophyta* and thus more closely related to the *Oomycota*, *Hyphochytridiomycota*, and *Labyrinthulomycetes* (Figure 1). Fungi are sessile (like plants) and heterotrophic organisms that are incapable of photosynthesis (like animals), with various strategies to obtain carbohydrates. These strategies range from the decomposition of dead organic material (saprotrophs) to attacking living organisms (pathogens, parasites, or carnivores) to forming different types of mutualistic symbioses with phototrophic plants, algae, and cyanobacteria (mycorrhizae and lichens) (Dix & Webster, 1995; Mueller *et al*., 2004; Piepenbring, 2015; Watkinson *et al*., 2016). Endophytic and endolichenic fungi are ubiquitous as asymptomatic inhabitants of plants, plant-like organisms, and lichens (Rodriguez *et al*., 2009; U'Ren *et al*., 2012). They are often classified as symbionts (e.g., in the FUNGuild database; Nguyen *et al*., 2016), but their biological roles are diverse and often unknown, and they should only be considered symbionts if there is actual evidence for this (Arnold & Lewis, 2005; Bolívar-Anillo *et al*., 2016; Bastias *et al*., 2021). Indeed, the diversity of potential life forms of endophytic and endolichenic fungi has been dubbed the "endophytic continuum" (Schulz & Boyle, 2005).

Although mostly invisible ("ecologically hidden"), fungi are crucial components of most ecosystems on earth, being particularly involved in nutrient cycling (Dix & Webster, 1995; Watkinson *et al*., 2016). In addition, they have played, and continue to play, important roles in ancient and modern cultures (Guzmán *et al*., 2003; Dugan, 2008). These include their uses as food, in industrial, biotechnological, and pharmaceutical applications, and in biomonitoring and mycoremediation (Nimis *et al*., 2002; Rhodes, 2014; Hyde *et al*., 2019; see also Chapter 13).

Fungi also hold several records among living organisms. For instance, species of *Armillaria* (honey mushrooms) form several of the largest known single organisms on earth, with biomasses corresponding to up to three blue whales (Smith *et al*., 1992; Schmitt & Tatum, 2008; Anderson *et al*., 2018). The widespread *Schizophyllum commune* (split gill) and *Coprinopsis cinerea* (gray shag), both model fungi, have been shown to develop more than 20,000 mating types or "sexes" (Kothe, 1999; Casselton & Kües, 2007). The lichenised fungus *Buellia frigida* in dry valleys of Antarctica forms thalli that are among the oldest documented organisms on earth, in part estimated at over 6,500 years old (Green *et al*., 2012).

In terms of known species, *Fungi* currently rank third amongst the three large kingdoms, with 150,000 species (Lücking *et al*., 2021a), after *Animalia* (animals), with 1.66 million known species (Zhang, 2013), and *Viridiplantae* (plants), with at least 350,000 known species (Christenhusz & Byng, 2016; The Plant List, 2021). *Fungi* are clearly the least well-known of these three kingdoms, given that estimates predict a much higher number of species, between 1.5 and 6.3 million (Blackwell, 2011; Hawksworth & Lücking, 2017; Baldrian *et al*., 2021). These estimates would place *Fungi* as the second-largest kingdom after animals, including estimates for unknown arthropods (see below), but far ahead of plants. Predictive estimates of global fungal diversity are based on diverse considerations, including a mean global fungi:plant species ratio of between 6:1 and 10:1, but also taking into account accumulating evidence of hidden diversity among presumably known species, with a mean ratio of over 10:1, as well as a wealth of data emerging from environmental sequencing studies (Baldrian *et al*., 2021; Lücking *et al*., 2021a). Cataloguing this unknown diversity is the major challenge for mycology in terms of time and resources and how to deal with fungi only known from sequence data (Lücking *et al*., 2021a). Much of this unknown fungal diversity is expected to be found in tropical regions, such as Colombia.

DIVERSITY OF FUNGI OF COLOMBIA IN THE TREE OF LIFE

The Col*Fungi* project (Gaya *et al*., 2021; https://colfungi.org) represents the first compilation of data on all groups of fungi of Colombia into a single resource, including nomenclatural and taxonomic checks. This project resulted in a total of 7,241 accepted species of fungi for Colombia, encompassing a high diversity of fungal life forms, including mushrooms and lichen-formers, plant- and animal-pathogenic microfungi, moulds, yeasts, among many others (Figure 2). By itself, the number of 7,241 species is difficult to evaluate, but when put into a taxonomic and geographic context, it illustrates the current state of knowledge of the Colombian funga.

Country- or region-based comparisons of biodiversity are often presented in the context of global conservation approaches, but these listings are usually limited to plants and vertebrates (mammals, birds, reptiles, amphibians, and fish; e.g., Butler, 2016, 2019), whereas fungi are rarely included in such comparisons. Colombia is currently ranked second among the ten most biodiversity-rich countries in plant and vertebrate species richness, trailing Brazil but ahead of Indonesia, China, Mexico, Peru, Australia, India, Ecuador, and Venezuela (Butler, 2016, 2019). According to these listings, Colombia has 51,220 plant species, 2,053 fish, 1,878 birds, 771 amphibians, 601 reptiles, and 442 mammals, and updated numbers for all vertebrate groups are consistently higher (Table 1). Notably, with 7,241 known species, fungi would rank second in this enumeration for Colombia.

Still, this ranking would be misleading: plants and fungi essentially represent entire kingdoms, whereas, in terms of

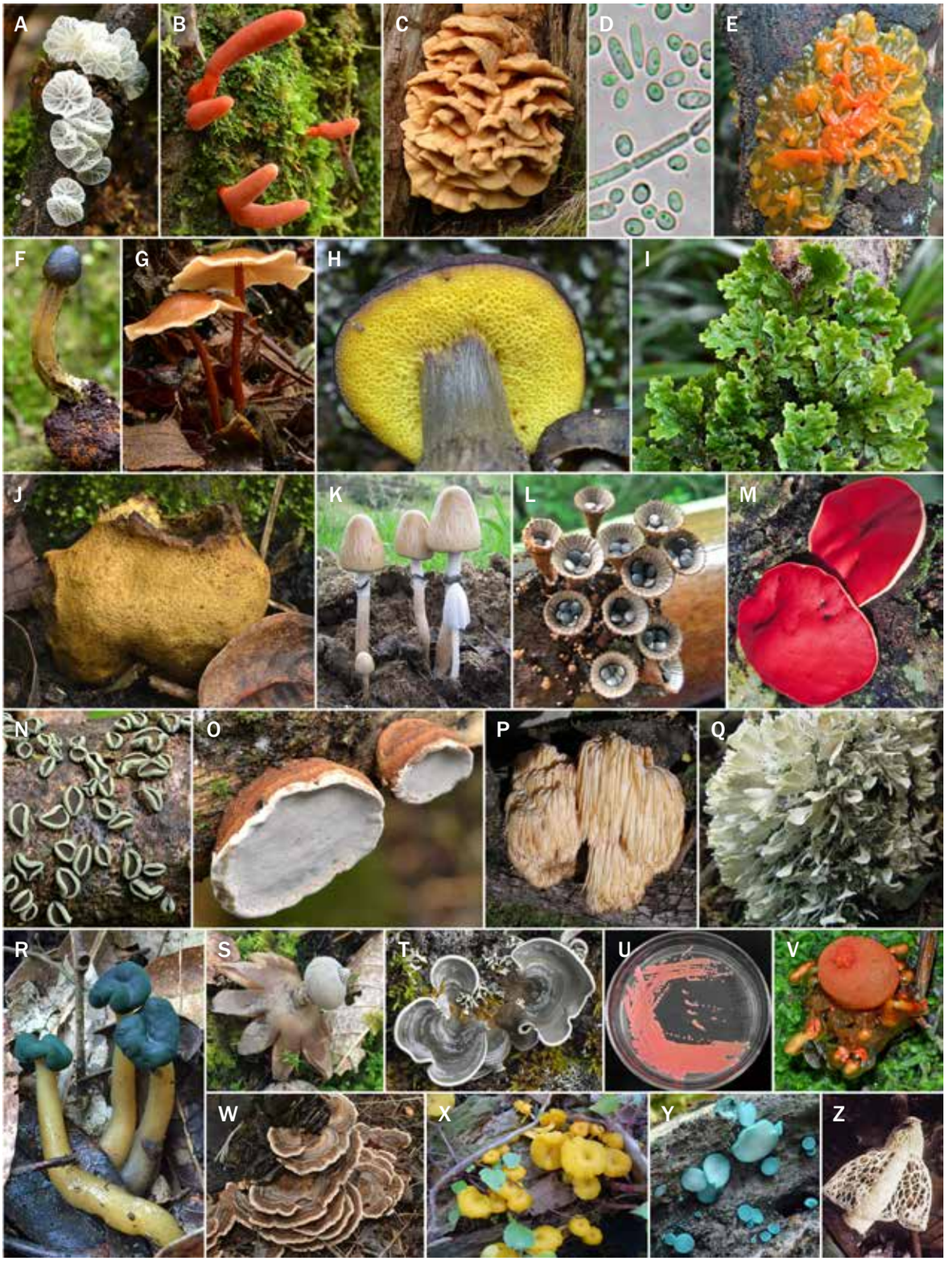

FIGURE 2. Examples of fungi of Colombia representing a diversity of lifestyles and phenotypes of spore-bearing structures. **A** *Campanella caesia*. **B** *Cordyceps nidus*. **C** *Laetiporus sulphureus*. **D** *Candida* sp. **E** *Auricularia mesenterica*. **F** *Tolypocladium capitatum*. **G** *Laccaria laccata*. **H** *Boletus* sp. **I** *Yoshimuriella peltigera*. **J** *Scleroderma flavidum*. **K** *Panaeolus semiovatus*. **L** *Cyathus striatus*. **M** *Phillipsia domingensis*. **N** *Rhytidhysteron columbiense*. **O** *Cerioporus scutellatus*. **P** *Hericium erinaceus*. **Q** *Hydnopolyporus fimbriatus*. **R** *Leotia lubrica*. **S** *Geastrum pectinatum*. **T** *Cora elephas*. **U** *Rhodotorula* sp. **V** *Calostoma cinnabarinum*. **W** *Trametes versicolor*. **X** *Collybia plectophylla*. **Y** *Chlorociboria aeruginascens*. **Z** *Phallus indusiatus*. Photographs: A, B, C, F, G, I, J, N, O, Q, T, W, Y: Robert Lücking. D, U: Mauricio Ramírez. E, L, R, S: Aída Vasco-Palacios. H, V: Bibiana Moncada. K, M, P, Z: Ana Esperanza Franco-Molano. X: Ana Cristina Bolaños.

TABLE 1. Updated totals for the number of known species of selected groups of organisms in Colombia. The global totals exclude fossil taxa.

Group	Butler (2016, 2019)	Updated figures	Global total	Proportion of updated figures vs global total	Reference(s) for updated figures
Animals	—	—	1,530,000	—	Zhang (2013); this paper
Vertebrates	5,745	7,607	57,102	13.2%	This paper
Fish	2,053	3,700	32,000	11.6%	Mejia & Acero (2002); Maldonado-Ocampo *et al*. (2008); Nelson *et al*. (2016); DoNascimento *et al*. (2018)
Amphibia	771	836	8,348	10.0%	Acosta-Galvis (2019); Frost (2021)
Reptiles	601	634	11,440	5.5%	Uetz *et al*. (2021)
Birds	1,878	1,909	9,159	20.8%	Barrowclough *et al*. (2016); Avendaño *et al*. (2017)
Mammals	442	528	6,451	8.2%	Burgin *et al*. (2018); Mammal Diversity Database (2021)
Invertebrates					
Insects	—	68,000	1,000,000	6.8%	This paper
Papilionoidea	—	3,642	18,768	19.4%	Garwood *et al*. (2021)
Formicidae	—	1,100	13,809	8.0%	Fernández *et al*. (2019); Bolton (2020)
Staphylinidae	—	800	48,000	1.7%	Newton *et al*. (2005)
Cicadellidae	—	679	22,000	3.1%	Freytag & Sharkey (2002)
Odonata	—	335	6,000	5.6%	Pérez-Gutiérrez & Palacino-Rodríguez (2011)
Blattaria	—	133	4,330	3.1%	Vélez (2008)
Arachnida	—	1,546	57,126	2.7%	Perafán *et al*. (2013)
Plants	51,220	26,150	350,000	7.5%	Bernal *et al*. (2016a, b, 2019); Diazgranados *et al*. (2021); The Plant List (2021)
Vascular plants	—	24,500	316,000	7.8%	Bernal *et al*. (2016a, b, 2019); Diazgranados *et al*. (2021); The Plant List (2021)
Bryophytes	—	1,650	34,500	4.8%	Bernal *et al*. (2016a, b, 2019); Diazgranados *et al*. (2021); The Plant List (2021)
Fungi	—	7,241	150,000	4.8%	Gaya *et al*. (2021); Lücking *et al*. (2021a); this paper
Ascomycota	—	4,564	93,632	4.9%	Gaya *et al*. (2021); Kirk (pers. comm. July 2021); this paper
Basidiomycota	—	2,318	50,460	4.7%	Gaya *et al*. (2021); Kirk (pers. comm. July 2021); this paper

species richness, vertebrates are only a small fraction of the animal kingdom, the diversity of which is concentrated among arthropods (Stork, 2018). Indeed, the known insect diversity of Colombia alone should easily surpass that of vertebrates and likely even plants. For instance, Newton *et al*., (2005) listed nearly 800 species only of *Staphylinidae* (rove beetles) for the country, out of a total of 48,000 known globally, and Vélez (2008) enumerated 133 species of *Blattaria* (cockroaches), compared to 4,330 worldwide (Table 1). Pérez-Gutiérrez & Palacino-Rodríguez (2011) reported 335 species of *Odonata* (dragonflies), out of a global total of around 6,000. For *Formicidae* (ants), Fernández *et al*., (2019) listed 1,100 species for Colombia, compared to over 13,800 globally (Bolton, 2020). The most comprehensive and most recent checklist of Colombian butterflies (*Papilionoidea*) compiled data on 3,642 species out of a global number of 18,768 (Garwood *et al*., 2021). According to Stork (2018), about one million insect species have been named, which means that globally, *Staphylinidae* corresponds to 4.8%, *Papilionoidea* 1.9%, *Formicidae* 1.4%, *Odonata* 0.6%, and *Blattaria* a little over 0.4% of that number. Extrapolating from these proportions in the case of Colombia implies that a total of between 17,000 and 194,000 insect species are likely known from the country, with a median of 43,350 and a mean of 68,000 (Table 1). Although the exact number has not yet been compiled, this extrapolation is far ahead of the

7,241 fungi and even ahead of the actual known number of plant species (see below).

Compared to the 51,220 species of plants reported for Colombia (Butler, 2016, 2019), the number of 7,241 fungal species also appears relatively low, with a fungus:plant species ratio of 1:7. However, the figure of 51,220 plant species goes back to outdated sources, being recently corrected to about 26,150 species in the *Catálogo de Plantas y Líquenes de Colombia* (Bernal *et al*., 2016a, b, 2019) and the most recent compilation of Col*Plant*A (Diazgranados *et al*., 2021). Based on the corrected number, Colombia's fungus:plant species ratio currently amounts to about 1:3.6, still much lower than ratios of between 6:1 and 10:1 obtained from well-studied extra-tropical areas (Hawksworth & Lücking, 2017). In terms of global diversity, Colombia harbours 4.8% of the 150,000 known fungal species and 7.5% of the 350,000 known plant species (Table 1). While these percentages are in the same order of magnitude, they do not consider the much more limited state of knowledge of global fungal diversity.

Fungi and fungus-like organisms are currently arranged into 64 classes (Species Fungorum 2021), of which 36 have been reported from Colombia. The remaining 28 classes are species-poor, with between one and 321 species globally. These remaining classes potentially occur in Colombia but are challenging to detect, as they largely represent ecologically hidden microfungi. Among the 36 classes present in Colombia, 11 are overrepresented compared to global proportions, by a factor of up to 6.5 (Figure 3). The seven most overrepresented classes are *Glomeromycetes* (factor 6.5), *Coniocybomycetes* (3.9), *Mortierellomycetes* (4.3), *Schizosaccharomycetes* (4.0), *Lecanoromycetes* (3.8), *Candelariomycetes* (3.8), and *Arthoniomycetes* (3.6). Four of these seven classes have low species numbers in Colombia, between one and 26, so the observed deviations are not meaningful, but the three remaining classes are represented by higher species numbers: *Lecanoromycetes* (2,167), *Arthoniomycetes* (189) and *Glomeromycetes* (106). The substantial overrepresentation of *Lecanoromycetes* and *Arthoniomycetes* is because these mostly lichen-forming fungi are much better studied than any other larger group of fungi in Colombia (Gaya *et al*., 2021), so the observed deviations are based on study bias. On the other hand, five important classes that are highly diverse in tropical regions but substantially underrepresented and understudied in Colombia are *Dothideomycetes*, *Sordariomycetes*, *Leotiomycetes, Pezizomycetes*, and *Laboulbeniomycetes* (Figure 3).

DIVERSITY OF FUNGI OF COLOMBIA IN A GLOBAL CONTEXT

Knowledge on organismic diversity is unevenly distributed across the planet, and even the absolute state of knowledge is opposed to the estimated diversity in a region. This scenario is largely because there are more specialists per area working in regions with fewer species per area for almost any group of organisms, particularly fungi (Hawksworth, 2001; Piepenbring *et al*., 2018). As a result, in biodiversity-rich countries, such as Colombia, even though the number of fungal species is expected to be higher than in extra-tropical areas, the absolute number of mycological studies is much lower. For instance, a search in the *Web of Science* [https://www.webofscience.com/wos/woscc/basic-search], using the string <(ALL=(Fungi)) AND ALL=(Country)>, retrieved around 16,000 results between 1900 and 2020 for the U.K. (England, Northern Ireland, Scotland, Wales), but only 1,155 for Colombia. Unfortunately, reliable estimates of known fungal diversity are difficult to obtain for most countries due to the lack of comprehensive databases or checklists, exceptions being lichenised fungi and macrofungi (Feuerer & Hawksworth, 2007; Gaya *et al*., 2021). Also, the nature and detail of existing compilations may differ markedly between countries, making comparisons challenging. Nevertheless, we attempted to compile existing data to compare Colombia with selected countries within and outside the tropics (see Gaya *et al*., 2021; here updated).

The highest number of fungi, including all lifestyles, has been reported for the United States (Table 2), with approximately 45,000 species (Perlmutter & Weakley, 2018; Bates *et al*., 2018; Esslinger, 2019). However, this impressive number is tentative, as, for non-lichenised fungi, current names and synonyms have not been fully sorted out. After India, with 29,000 species, France remarkably ranks third, with 24,840 species, followed by China (23,927) and Italy (22,700) (Roux, 2012; Onofri *et al*., 2013; Medardi, 2006; Venturella *et al*., 2011; Nimis, 2016; Institute of Microbiology, Chinese Academy of Sciences, 2018; Gargominy *et al*., 2020; Wang *et al*., 2020; Wei, 2021). We had originally reported 20,500 species for Brazil (Gaya *et al*., 2021), but a reanalysis of the underlying data, including accepted names vs synonyms, led to a correction, with now 13,950 species (see Table 2). This number is still substantially higher than the 5,719 species reported by Maia *et al*., (2015), the latter likely an underestimate based on an incomplete list of selected records for particular groups.

Among the countries assessed here, Colombia ranks seventh for lichenised fungi (see Chapter 6). In comparison, the overall number and particularly the number of non-lichenised fungi is comparatively low, with Colombia currently taking 13th place. In terms of species density and species per $\log_{10}$(area), Colombia also ranks comparatively low, particularly when compared to its richness in other groups of organisms, leading us to the question: how many species of fungi can we expect in Colombia?

HOW MANY SPECIES OF FUNGI ARE THERE IN COLOMBIA?

Predictive estimates of species richness are naturally speculative, especially for ecologically largely hidden organisms and in groups where taxon concepts have not been fully resolved. Several approaches exist to predict species numbers on the basis of known species and other data. One possible approach is the assumption that Colombia's species per $\log_{10}$(area) estimate should be

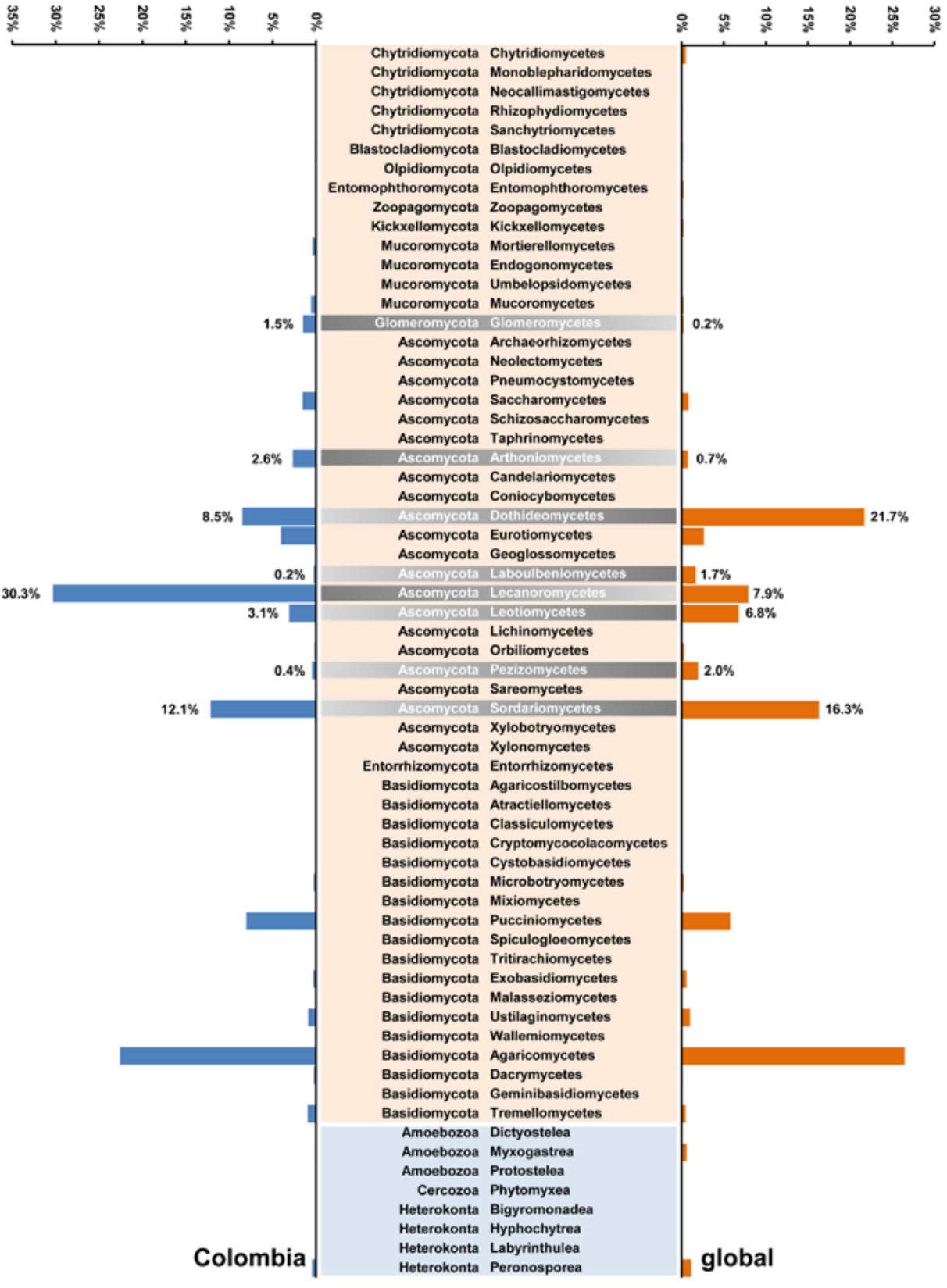

FIGURE 3. Comparison of the proportional phylogenetic diversity of *Fungi* and fungus-like organisms at the class level between Colombia and the global funga. The percentages indicate the number of species per class compared to the corresponding total. Selected classes that are over- or underrepresented in Colombia are marked in dark grey, and the corresponding percentages are indicated. For detailed data, see Suppl. File S1.

TABLE 2. Comparison of numbers of known fungal species between selected countries. The number of 16,900 macrofungi for the United States is an estimate based on Bates *et al*. (2018). The corrected total for Brazil (13,950; as compared to 20,500 reported in Gaya *et al*., 2021) is based on the accepted number of fungal names for Brazil on SpeciesLink (approximately 11,330), minus the number of lichenised species in that database (approximately 1,690), plus the updated number of lichenised species based on Aptroot (2021).

Country / Territory	All fungi	Lichenised fungi	Macro-fungi	Density [species / log10(km^2)]	Reference(s)
United States	45,000	4,341	16,900	6,578	Perlmutter & Weakley (2018); Bates *et al*. (2018); Esslinger (2019)
India	27,000	2,714	—	4,450	Sarbhoy *et al*. (1996); Singh & Sinha (2010); Manoharachary & Nagaraju (2016); Sinha *et al*. (2018)
France	24,840	2,917	—	4,276	Roux (2012); Gargominy *et al*. (2020)
China	23,927	3,050	7,138	3,427	Institute of Microbiology, Chinese Academy of Sciences (2018); Wang *et al*. 2020; Wei (2021)
Italy	22,700	2,704	4,198	4,143	Onofri *et al*. (2013); Medardi (2006); Venturella *et al*. (2011); Nimis (2016); Checklist of Italian Fungi (2021)
United Kingdom	20,000	2,000	3,100	3,343	Legon & Henrici (2005); Smith *et al*. (2009); Dines & McCarthy (2014); Clubbe *et al*. (2020)
Germany	15,295	1,946	6,120	2,754	Wirth *et al*. (2011); DGfM (2021)
Japan	14,000	1,906	4,160	2,510	Hosoya (2006); Katumoto (2009); Ohmura & Kashiwadani (2018)
Brazil	13,950	4,310	2,300	2,013	Lewinsohn & Prado (2005); Maia *et al*. (2015); Aptroot (2021); SpeciesLink (2021)
Australia	12,870	4,003	4,000	1,869	May *et al*. (2004); McCarthy (2020)
Canada	12,800	2,262	4,500	1,829	Perlmutter & Weakley (2018); Bates *et al*. (2018); Esslinger (2019)
Venezuela	8,300	1,801	—	1,392	Marcano *et al*. (1996); Itturiaga (2000); Hernández-M. (2021)
Mexico	7,632	2,722	2,900	1,212	Guzmán (1998a, b); Cifuentes (2008); Aguirre-Acosta *et al*. (2014); Herrera-Campos *et al*. (2014); Bates *et al*. (2018)
Colombia	7,241	2,559	1,239	1,210	Vasco-Palacios & Franco-Molano (2013); Gaya *et al*. (2021); Lücking *et al*. (2021b); this paper
Thailand	7,300	1,292	2,100	1,278	Hywel-Jones & Boonpratuang (2001); Chandrasrikul *et al*. (2011); Buaruang *et al*. (2017); Hyde *et al*. (2018); Index Fungorum (2021)
Malaysia	3,804	—	—	689	Chua *et al*. (2012)
Costa Rica	3,500	1,740	2,000	743	Halling & Mueller (2005); Mueller *et al*. (2007)
Bolivia	2,234	1,353	500	370	Piepenbring (2004); Rodriguez de Flakus *et al*. (2016); Melgarejo-Estrada *et al*. (2020a, b)
Panama	1,807	325	300	370	Piepenbring (2007)

comparable to that of a well-studied temperate country, such as the United States. Colombia encompasses an area of 1.143 million km^2, compared to 9.834 million km^2 for the United States. The latter has 6,578 fungal species per $\log_{10}$(km^2), so with $\log_{10}$(1,143,000) = 6.058, one would expect 6,578 x 6.058 = 39,850 species for Colombia (Table 3). This figure is about 5.5 times higher than the currently known number. Given that lichen-forming fungi have been estimated at nearly 5,000 species for Colombia (see Chapter 6), this would result in approximately 35,000 species of non-lichenised fungi. Since about 5,000 species of non-lichenised fungi are known from Colombia (Gaya *et al*., 2021), nearly 30,000 still need to be catalogued. However, the actual number could be even higher because tropical ecosystems on average support higher small-scale species richness than temperate areas, which means that patterns found in the United States or other largely temperate countries cannot be directly transferred.

TABLE 3. Various predictions of the actual species richness of the Colombian funga using different approaches.

Prediction	Approach
27,430	Adjusted according to a proportion of well-studied class *Lecanoromycetes*
39,850	Species versus $\log_{10}$(area) relationship using the USA as a benchmark
105,600 –182,400	Colombian proportion of global estimated richness, using known fungi as a benchmark (4.8%) and 2.2–3.8 million estimated fungal species globally (Hawksworth & Lücking, 2017)
156,900 –261,500	Fungi:plant ratio between 6:1 and 10:1
165,000 –285,000	Colombian proportion of global estimated richness, using known plants as a benchmark (7.5%) and 2.2–3.8 million estimated fungal species globally (Hawksworth & Lücking, 2017)
220,000 –380,000	Colombian proportion of global estimated richness, using known amphibia as a benchmark (10.0%) and 2.2–3.8 million estimated fungal species globally (Hawksworth & Lücking, 2017)

A similar prediction is achieved when considering the phylogenetic diversity of fungi of Colombia at the class level (Figure 3). As outlined above, the largest overrepresented class is *Lecanoromycetes* (30.3% in Colombia versus 7.9% globally), which includes most of the lichenised fungi, a group particularly well-studied in Colombia. If we assume that the global proportion of *Lecanoromycetes* is relatively constant across terrestrial ecosystems dominated by woody plants, then Colombia would be expected to harbour at least 27,430 species of fungi to render the current number of 2,167 *Lecanoromycetes* at a proportion of 7.9%.

Another approach is to look at proportional richness per organism group in Colombia relative to the known global diversity of the group. The observed values range between 4.3% for insects and 20.8% for birds, with others in between, e.g., 7.5% for plants, 8.2% for mammals, and 10.0% for amphibia (Table 1). Relying on well-studied groups and taking into account how species in particular groups can successfully disperse, that is, how sizable average species ranges probably are, for fungi, one could assume values similar to those of plants or amphibia (or butterflies), that is, 7.5%–10.0% (–19.4%). The global estimate of between 2.2 and 3.8 million species (Hawksworth & Lücking, 2017) would give an estimate of (165,000–)220,000–285,000(–380,000) species for Colombia when applying the 7.5%–10.0% range (the 19.4% range probably being too high). Even taking the currently observed 4.8% for known Colombian vs globally known fungi as a basis, the estimate would range between 105,600 and 182,400 species, still much higher than the estimate based on $\log_{10}$(area) extrapolation (Table 3). Such estimates may seem unrealistic, but figures in the same order of magnitude, namely (100,000–)200,000(–260,000) species of fungi, have been proposed for Mexico (Guzmán 1998a, b; Aguirre-Acosta *et al*., 2014).

The fungus:plant species ratio is another commonly used measure for predictive species richness estimates (Martin, 1951; Hawksworth, 1991; Hawksworth & Lücking, 2017). Empirical data for this measure vary widely, ranging from 1.8:1 to 19.1:1, depending on the ecosystem and sampling methods. Thus, while plants within a given area can be sampled quite accurately, fungal sampling restricted to macroscopically visible fungi and within a limited time frame will naturally and often grossly underestimate fungal diversity, as evidenced by a study performed in Panama (Piepenbring *et al*., 2012). The ratio also depends on the group of fungi. For example, rust fungi (*Pucciniomycetes*) show lower empirical fungus:plant species ratios between 1:10 and 1:100, with more realistic ratios ranging between 1:4 and 1:20, resulting in estimates for the diversity of rust fungi alone in Colombia of between 2,500 and nearly 13,000 species (Salazar-Yepes & Alves de Carvalho Júnior, 2013). However, these approaches have largely not been tested using molecular approaches, both in terms of taxon concepts in rust fungi and the detection of species not producing spore-bearing structures. In addition, fungus:plant species ratios vary with latitude, higher ratios in temperate areas going along with substantially lower plant diversity, which requires a downwards correction when extrapolating globally (Tedersoo *et al*., 2014). Estimates may be further misguided by outdated numbers for plant diversity, such as the earlier - reported exaggerated figure of 51,220 plant species for Colombia (see above). Studies that include more sophisticated sampling methods, such as long-term plots and/or metabarcoding, show overall fungus:plant species ratios of between 6:1 and 10:1. However, such studies have been mostly restricted to temperate ecosystems (Hawksworth & Lücking, 2017). Given the number of 26,150 plant species currently known from Colombia, applying the fungus:plant species ratio approach would thus result in 156,900–261,500 species of fungi for Colombia, a figure comparable to that derived from the proportional richness approach (Table 3).

Although a reliable estimate of fungal diversity in Colombia remains speculative, we can safely assume that the predicted figure is perhaps an order of magnitude higher than the currently number of known species. Apart from the sheer size of that number, the more daunting perspective is the effort required to document this largely unknown diversity, requiring a large task force of experts in the different fungal groups and consequent application of modern methods of biodiversity research. Unfortunately, molecular approaches to catalogue fungi are still limited in Colombia. We performed a structured search in the NCBI GenBank [https://www.ncbi.nlm.nih.gov/genbank], using the string <Fungi[organism] AND (5.8S[title] OR ITS1[title] OR ITS2[title] OR “internal

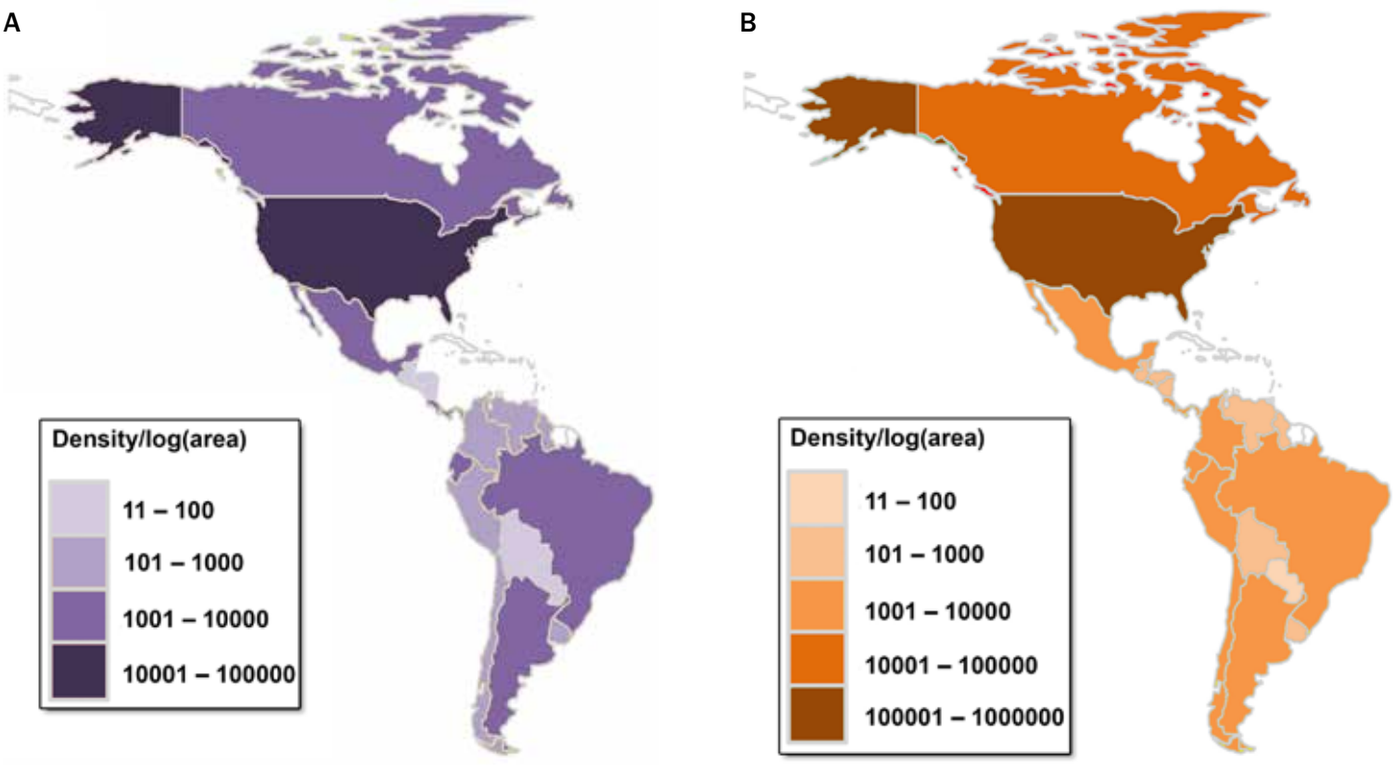

FIGURE 4. Number of NCBI GenBank accessions obtained using the fungal ITS barcoding marker (**A**) and number of biosamples from metabarcoding studies using various markers (**B**), adjusted for area size [relative to $\log_{10}$(area)] for countries across the Americas.

transcribed spacer"[title]) AND country>, for all countries in the Americas, to assess how many accessions of the fungal ITS barcoding marker exist for each country, and then divided the number by $\log_{10}$(area), to filter the area effect. The United States ranks two orders of magnitude ahead of Colombia, whereas Canada, Mexico, Costa Rica, Ecuador, Brazil, and Argentina rank one order of magnitude ahead (Figure 4A). We further queried the NCBI Sequence Read Archive [https://www.ncbi.nlm.nih.gov/sra] using the country name and recording the number of resulting biosamples, also dividing them by log10(area) to obtain an estimate of existing metabarcoding studies. Again, the United States ranges two orders of magnitude ahead of Colombia and most other countries except Canada (Figure 4B).

Considering that it took about 200 years to arrive at a list of just 7,241 species of fungi known from Colombia using mostly traditional inventory methods, efforts have to be increased by about two orders of magnitude to catalogue an additional at least 30,000 species within a reasonable time frame of 15–20 years. For this to happen, there needs to be a paradigm shift in the political and societal support for this kind of work in Colombia, and across Latin America and other tropical regions in general.

CONCLUSIONS

The first assembly of a critical checklist of the Colombian funga is a milestone in the state of knowledge of fungi in the country. However, compared to other organisms and in a global context, the inventory of fungi of Colombia is still at its onset in terms of expected numbers. Although a good balance of taxonomic groups has been studied to date in Colombia, including a wide array of macro- and microfungi and fungi representing different lifestyles, the development of mycology is not at a level comparable to that in temperate countries, in which non-professional mycology also plays a critical role in performing inventory work. We believe that mycology in Colombia can only develop further if the focus is not only on applied approaches, but more resources are provided for basic scientific studies, allowing the adoption of modern technologies, such as molecular (meta-)barcoding at a broader scale. In parallel, fostering taxonomic specialist groups for the various taxa is necessary, particularly for taxa that remain grossly understudied. The formation of associations, such as the *Asociación Colombiana de Micología* (ASCOLMI) and the *Grupo Colombiano de Liquenología* (GCOL) can be considered an excellent initiative to achieve this goal.

Acknowledgements

Paul Kirk is warmly thanked for putting data from *Index Fungorum* and *Species Fungorum* at our disposal and for assistance with obtaining data on the checklist of fungi from China. Kevin Hyde, Gareth Jones, and Gary Perlmutter assisted with obtaining references regarding fungal diversity in Thailand, Malaysia, and North America. Meike Piepenbring and Mauricio Salazar-Yepes provided thoughtful reviews that helped to improve this chapter, and Rafael Felipe de Almeida assisted in linguistic editing.

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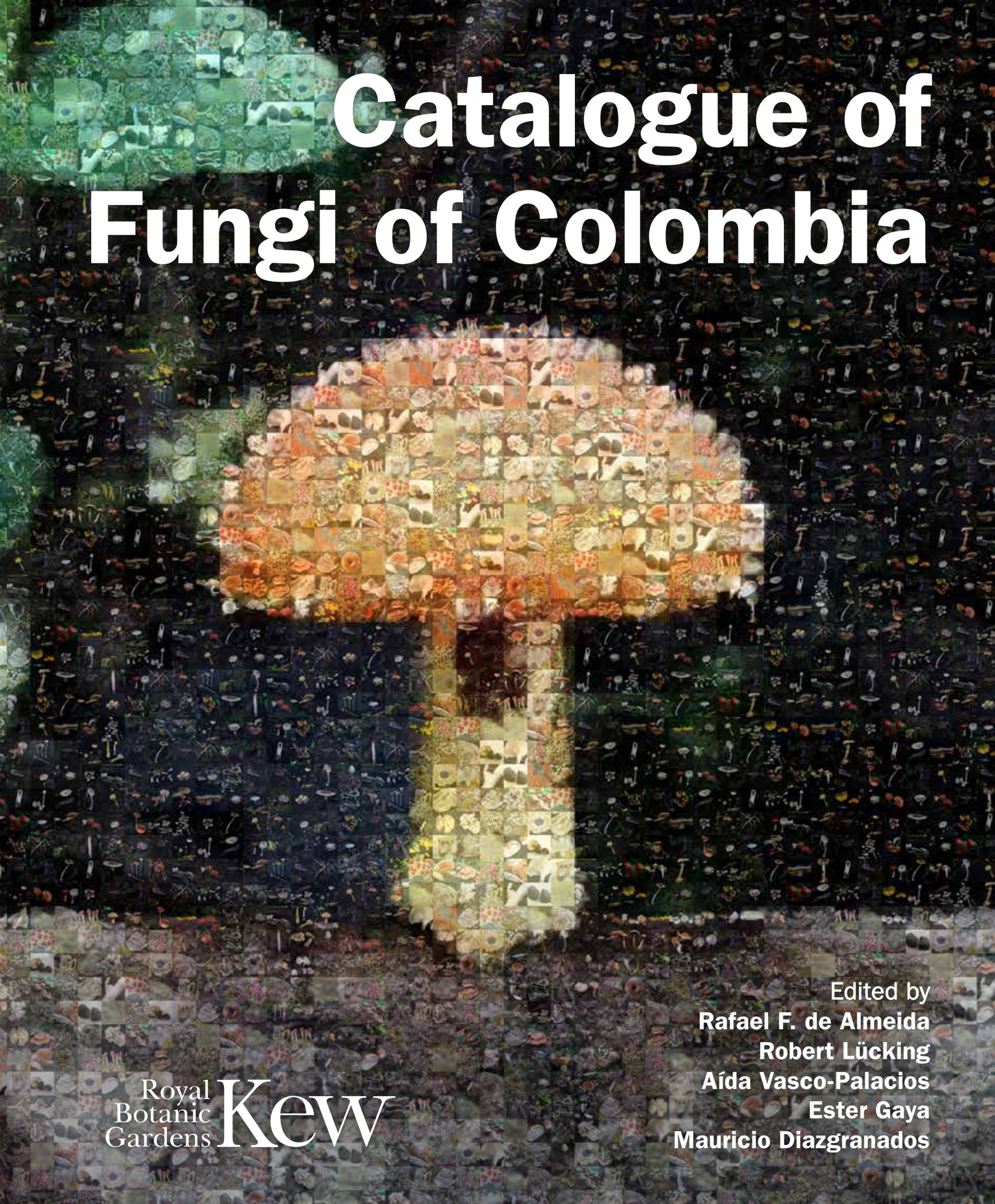

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Royal Botanic Gardens Kew

First published in 2022 by Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, UK, in association with the Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Calle 28A #16-29, Bogotá, Colombia.
www.kew.org

ISBN 978-1-84246-790-9
eISBN 978-1-84246-791-6

Distributed on behalf of the Royal Botanic Gardens, Kew in North America by the University of Chicago Press, 1427 East 60th Street, Chicago, IL 606037, USA.

British Library Cataloguing in Publication Data
A catalogue record for this book is available from the British Library.

Design: Nicola Thompson, Culver Design
Production Manager: Jo Pillai
Proofreading: Sharon Whitehead

Printed in Great Britain by Halstan & Co Ltd

For information or to purchase all Kew titles please visit shop.kew.org/kewbooksonline or email publishing@kew.org
For Instituto Humboldt publications visit http://repository.humboldt.org.co/

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Kew receives approximately one third of its funding from Government through the Department for Environment, Food and Rural Affairs (Defra).
All other funding needed to support Kew's vital work comes from members, foundations, donors and commercial activities, including book sales.

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Funded by:

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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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ISBN 978–1–84246–790–9

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