



Chapter 10

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Author Contributions: AVP and RL contributed to the conception of the manuscript; VMV and MP wrote the Biogeography of Colombian polypores section; AVP wrote the Biogeography of Colombian ectomycorrhizal fungi section; and BM and RL wrote the lichenized fungi, Biogeography of Colombian lichens: traditional taxonomy versus molecular data section.

Keywords: cryptic species, dispersal, ectomycorrhizae, Gondwanan lineages, Holarctic lineages, lichenised fungi, neotropical distribution, vicariance, saprotroph.

ABSTRACT

This chapter attempts to assess the distribution patterns of three selected groups of fungi, namely polypores, ectomycorrhizal fungi (EcM), and lichenised fungi in Colombia. Assessing the biogeography of fungi is difficult because of two key issues: 1. information gaps on their distribution and biology in biodiversity-rich countries, such as Colombia, and 2. the traditional, phenotype-based species concepts, which make it difficult to recognise cryptic species or species complexes. This latter aspect is very frequent in fungi, as currently revealed by advanced molecular biology and phylogenetic analysis techniques. For instance, *Polyporus* is a widespread genus, commonly found in Colombia with numerous species recorded as cosmopolitan. However, detailed studies in some *Polyporus sensu lato* in Brazil and Argentina showed a hidden diversity now accommodated in different genera such as *Atroporus*, *Neodictyopus*, and *Bresadolia*. On the other hand, the various fungal lineages show different distribution patterns depending on their biology. This fact evidences how the biogeographic distribution of ectomycorrhizal symbiont fungi (EcM) is closely linked with the distribution patterns of their host plants, but due to information gaps, their real distribution ranges are unknown. It has been observed that the EcM fungi associated with Fagaceae in the Andean region belong to Holarctic lineages, while the species associated with the Fabaceae or Dipterocarpaceae in the Colombian Amazonia Region come from tropical lineages of Gondwanan origin. Finally, for lichenised fungi, we looked at eight genera in four families and two classes and phyla: *Bunodophoron* (Sphaerophoraceae), *Neoprotoparmelia* (Parmeliaceae), *Crocodia*, *Lobariella*, *Podostictina*, *Pseudocyphellaria*, *Sticta* (Peltigeraceae, all Ascomycota), and *Cora* (Hygrophoraceae, Basidiomycota). Comparing traditional taxonomy with modern taxon concepts derived from integrative approaches using molecular and phenotype data revealed that the proportion of distribution types assessed from the data changed substantially. When using a traditional taxon concept, 45% of the species were inferred to have a broad, intercontinental distribution, 39% neotropical, and 12% endemic. On the other hand, using the modern taxon concept indicated that only 4% of them were widespread, 20% neotropical, and 76% potentially endemic. These findings underline the importance of accurate taxon concepts and proper knowledge of evolutionary relationships when performing biogeographical analyses of Colombian fungi. As mycologists, we must then continue to generating information that allows us to understand the historical processes responsible for the geographical distributions of the different lineages of fungi present in the national territory.

RESUMEN

La biogeografía se encarga de los patrones de distribución global de los organismos, dilucidando los factores y procesos que conducen a estos patrones. Los estudios en esta área se han centrado en organismos macroscópicos, como plantas vasculares y vertebrados, dejando de lado microorganismos como bacterias, protistas, algas, plantas no vasculares y hongos. Por mucho tiempo se consideró que los microorganismos suponían rangos de distribución amplios e intercontinentales para muchas especies. El «todo está en todas partes» se aplicó durante décadas al pensar en la distribución de la mayoría de

los hongos. Sin embargo, los enfoques filogenéticos moleculares, combinados con el estudio de distribuciones y de las comunidades de hongos, han dejado ver que la biogeografía de los hongos es compleja. Estos procesos dependen tanto de la biología de las especies como de modelos de dispersión (expansión de las distribuciones) y vicarianza (fragmentación de las distribuciones), así como de la historia geológica de los continentes, i.e., migración de los hongos a través de puentes continentales, y la disyunción relictual continental. Muchas especies consideradas de distribución cosmopolita representan complejos de especies difíciles de diferenciar con caracteres morfológicos, pero visibles en análisis filogenéticos. Este es el caso del basidiolíqueno *Cora* y de las especies del grupo neotropical *Polyporus*. Como se ha explicado en capítulos anteriores, el conocimiento que tenemos hoy en día acerca de la diversidad, ecología, distribución, asociaciones y estado de conservación de los hongos en Colombia es aún incipiente, y esto dificulta entender y definir patrones de distribución de las diferentes especies presentes en el país. En este capítulo hacemos un primer acercamiento para evaluar los patrones de distribución de los hongos poliporoides comparando la riqueza y composición de las especies. Por ejemplo, en el género *Polyporus* son evidentes los sesgos existentes por la falta de estudios en el género *Polyporus* muestra los sesgos existentes por la falta de estudios que integren datos moleculares y análisis filogenéticos, este es el caso de especies que se pensaban ampliamente distribuidas como *Polyporus udus* y *Polyporus dictyopus*, las cuales se consideran complejos de especies e incluso representan géneros nuevos neotropicales, como es el caso de *Neodictyopus*. Por otro lado, diversos linajes de hongos muestran diferentes patrones de distribución. Así es como la distribución biogeográfica de los hongos simbioses ectomicorrízicos (EcM) está íntimamente ligada con los patrones de distribución de sus plantas hospederas, sin embargo, debido a los vacíos de información no se conocen los rangos reales de distribución. Se han reportado un total de 202 especies de hongos EcM en Colombia, de ellas, 56 son especies nuevas descritas a partir de especímenes colombianos y 36 son endémicas, lo que representa una tasa de endemismo de cerca del 20%. Sin embargo, hay que confirmar la distribución de muchas especies con registros antiguos que se conocen de pocos o de un único espécimen. En general se ha observado que los hongos EcM asociados a Fagaceae en la región Andina pertenecen a linajes holárticos, mientras que las especies asociadas a las familias Fabaceae o Dipterocarpaceae en la Amazonía Colombiana provienen de linajes tropicales de origen Gondwanico. Por último, se realizó un análisis con ocho géneros de líquenes y comparando conceptos de la taxonomía tradicional con conceptos de taxón modernos; i.e. derivados de enfoques integradores con datos moleculares y fenotípicos. Encontramos que la proporción de tipos de distribución evaluados a partir de los datos cambió sustancialmente. Al utilizar un concepto tradicional, se infirió un concepto tradicional, se infirió que el 45% de las especies tienen una amplia distribución intercontinental, 39% neotropical y 12% endémica. Mientras que, siguiendo un concepto moderno, solo el 4% tiene distribución amplia, el 20% neotropical y 76 % son potencialmente endémicas. Estos hallazgos subrayan la importancia de conceptos taxonómicos precisos y un conocimiento adecuado de las relaciones evolutivas al realizar análisis biogeográficos de hongos colombianos. Como micólogos, debemos seguir generando información que nos permita comprender los procesos históricos responsables de las distribuciones geográficas del pasado al presente de los diferentes linajes de hongos en el territorio nacional.

INTRODUCTION

Biogeography deals with the global distribution patterns of organisms and the factors and processes that underlie and lead to these patterns (Lomolino *et al.*, 2017). In the history of biogeographical studies, there usually has been a sharp distinction between macroorganisms, such as vascular plants and vertebrates, and microorganisms, such as bacteria, protists, fungi (including lichenised fungi) and even bryophytes. While macroorganisms were assumed to exhibit specific distribution patterns, allowing elaborate detailed classifications of biogeographic regions (Takhtajan *et al.*, 1986; Olson *et al.*, 2001), for microorganisms, it was generally assumed that “everything is everywhere” (Baas Becking, 1934; De Wit & Bouvier, 2006; O’Malley, 2007). The latter paradigm has frequently been applied for the biogeography of fungi by assuming broad and intercontinental distribution ranges for many species (e.g. Wicklow, 1981; Lücking, 2003; Feuerer & Hawksworth, 2007; Galloway, 2008; Werth, 2011; Ramírez-Camejo *et al.*, 2012; Aguilar *et al.*, 2014; Allen & Lendemer, 2015; Yang *et al.*, 2016). However, the more recent studies among these have pointed out that the biogeography of fungi is much more complex than that implied by such a simplified paradigm.

Molecular phylogenetic approaches, combined with the analysis of distribution patterns and community ecology, have made it possible to derive much more refined distribution patterns for species of fungi, resulting in many variations depending on which lineage and ecological traits are considered (Peay *et al.*, 2010; Summerell *et al.*, 2010; Tedersoo *et al.*, 2014; Song & Cui, 2017). In wood-decomposing polypores, cosmopolitan distributions are not rare, possibly explained by human dispersal through the global wood trade (Mueller *et al.*, 2006). However, this depends on individual cases and the methodological approaches, and on which genetic marker was sequenced. For example, when employing the fungal barcoding marker ITS (Schoch *et al.*, 2012), the widespread split gill fungus, *Schizophyllum commune* (Figure 1a–b), is considered a single species. Still, it shows a distinct geographic structure when employing the intergenic spacer (IGS), demonstrating that the global distribution of these fungi was originally not caused by humans (James *et al.*, 2001). A complex example in lichenised fungi is *Sticta fuliginosa*, a presumably cosmopolitan species forming conspicuous thalli. Molecular data revealed that what has been identified with this name for the past two centuries corresponds to at least 15 often distantly related species, many with restricted distributions



FIGURE 1. A–B *Schizophyllum commune* (split gill fungus) photographed in Colombia (A) and Germany (B). C–D *Sticta fuliginoides*, photographed in Colombia (C) and New Zealand (D). (Photographs by Robert Lücking.)

(Moncada *et al.*, 2014, 2020; Magain & Sérusiaux, 2015). Yet, the true *S. fuliginosa* remains a subcosmopolitan taxon, and a newly recognised taxon within this complex, *Sticta fuliginoides*, is also subcosmopolitan (Figure 1c–d). In microfungi, the situation is challenging: human-pathogenic fungi and those attacking widely utilised crops tend to become widespread following human-induced expansions of the host range and usually evolve into new regional lineages (Summerell *et al.*, 2010).

These issues make it extremely difficult to assess the overall biogeographical patterns of fungi in a biodiversity-rich country, such as Colombia, when relying primarily on phenotype-based or other taxonomic concepts, besides the fact that we do not know the total diversity of the Colombian fungi and the distribution of these species within and outside the country. This chapter refrains from deriving biogeographical patterns from the entire list of known fungal species. Instead, we focus on selected groups and specific examples to assess the realistic distribution patterns of species present in Colombia.

BIOGEOGRAPHY OF THE POLYPORES OF COLOMBIA

Polypores are a highly diverse group of fungi characterised by their growth form and ecology (Figure 2a–f), representing 2,300 species from the 21,000 species of Agaricomycetes within Basidiomycota (Kirk *et al.*, 2008). Species of polypores are found in various orders but are concentrated mainly in *Polyporales* and *Hymenochaetales*, which together contain around 80–90% of all polypores. These fungi are most diverse in forest ecosystems on all continents and are morphologically characterised by a typically poroid hymenophore and bracket-shaped to resupinate basidiomata. They almost exclusively occur as saprotrophs or parasites on dead or living trees, not rarely first attacking living trees and then continuing as saprotrophs on the dead trees. Only a few species grow on humus or mineral soil, and even fewer are mycorrhizal (Väisänen *et al.*, 1992; Tedersoo *et al.*, 2007). Polypores are the most critical wood decomposers, playing a pivotal role in forest ecosystems and their food webs by recycling wood, the most critical reservoir of organic carbon in the living world (Watkinson *et al.*, 2006, Krah *et al.*, 2018).



FIGURE 2. Fresh basidiomes of polypores. **A–B** Polyporaceae family. **A** *Polyporus tricholoma*. **B** *Polyporus dictyopus* species complex. **C** *Hydnopolyporus fimbriatus* (Irpicaceae). **D** *Ganoderma resinaceum* (Ganodermataceae). **E** *Flaviporus liebmanii* (Steccherinaceae). **F** *Hymenochaete iodina* (Hymenochaetaceae). (Photographs A, D by Melissa Palacio; B–C, E–F by Viviana Motato-Vásquez).

The species richness and composition of polypores are influenced by climate and tree species composition in forest ecosystems. Higher tree species diversity may result in higher polypore species richness (Hattori, 2017), and tropical forests are recognised for their high diversity of tree species – commonly hundreds of species within 50 ha areas (Condit *et al.*, 2000). However, assessing host specificity can become a challenge in such settings because it may be difficult to identify host species reliably, mainly when the basidiomata are produced on dead trees, fallen trunks, or high up in mature trees. Most polypore species are rare in species-rich tropical forests, whereas there is little evidence for host specificity in more common species (Lindblad, 2000; Gilbert *et al.*, 2002). Preferences for distinctive habitat types may be more important than host specificity in determining the distribution of polypores (Lindblad, 2001).

Despite significant efforts to characterise the richness of Neotropical fungi, resulting in essential checklists and inventories of Neotropical polypores (e.g. Carranza & Ruiz-Boyer, 2005; Silveira & Wright, 2005; Robledo & Rajchenberg, 2007; Baltazar & Gibertoni, 2009; Vasco-Palacios & Franco-Molano, 2013), the distribution patterns of polypores remain poorly known. Biogeographic studies on Neotropical polypores are scarce. For instance, De Lima *et al.* (2018) used polypores growing in the Brazilian rainforests to reconstruct biogeographical relationships between the Amazon Forest, Atlantic Forest, and Caatinga domains. Their results showed that polypores have distribution patterns similar to those of woody plants present in Brazilian rainforests. Another study was done with *Phellinotus piptadeniae* in the Neotropics (Salvador-Montoya *et al.*, 2015). This species is a parasitic polypore, causing heart-rot in some Fabaceae, with a disjunct distribution in moist and dry forests, including Argentina, Brazil, and Peru (Elias *et al.*, 2020). The study emphasised the importance of using host distributions in biogeographical analyses of parasitic polypores to assess distribution patterns. This fact illustrates another knowledge gap in Neotropical polypores, namely species biology, as it is often not known whether a species is parasitic or saprotrophic (or both), whether it causes white or brown rot, and whether it is a specialist or a generalist.

Based on accurate taxon concepts, the geographic distribution of species provides the data for biogeography, macroecology, and conservation science assessments. Species distributions are typically assessed through point records, either through human observation or ideally accompanied by voucher specimens that are permanently stored in scientific collections. Unfortunately, data about the geographic distribution of most fungi species known from Colombia are still insufficient, generating the so-called Wallacean knowledge shortfall, defined by the fact that geographical distribution for the majority of taxa is poorly understood and contains many gaps (Hortal *et al.*, 2015). This situation is particularly difficult for species less well-known than more charismatic species. Consequently, any effort to compile and analyse distributional data for Colombian polypores must be considered preliminary at this point.

We used a large, recently compiled database containing

all polypores recorded from Colombia, published through the ColFungi project (Gaya *et al.*, 2021; <https://colfungi.org>), assembling all (reliable) fungi species records for Colombia available in the taxonomic and biodiversity literature. With this dataset, we tried to answer accurately questions such as “where does this polypore species occur in Colombia?” Or even “how many polypore species are known to occur in this specific part (department, region, etc.) of Colombia?” Although we are still far from completing this goal, we hope to show the potential of our initiative in this case study.

A total of 84 genera and 223 polypore species have been recorded from different Colombian biomes (Figure 3a). However, the representation of data in this kind of map is limited as a tool to represent the distribution of species records (instead of representing species distribution *per se*). Each dot on this map can represent either a single record of a species or many records of several species collected at the same locality. Our data showed a high number of species with a single record (35.7% of the records, 80 species), which could be understood more as an index of sampling bias rather than as an indicator of the level of endemism.

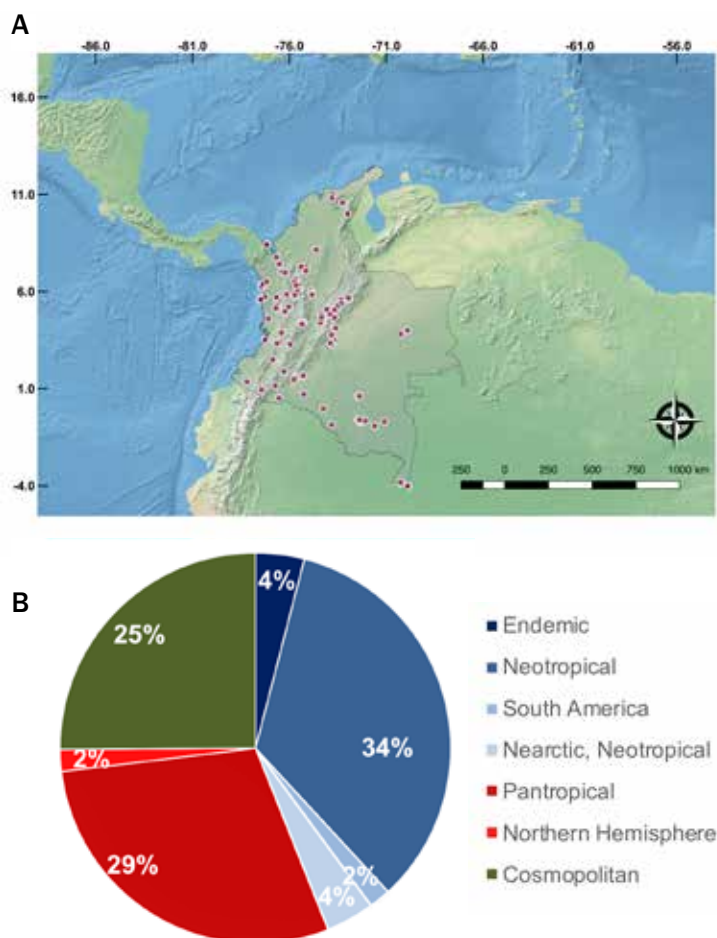


FIGURE 3. **A** Distribution and occurrence of records of polypore fungi in Colombia. Each dot represents at least one record of a single species. **B** Main areas of the geographical distribution of the 223 species of polyporoid fungi registered in Colombia. Blue tones indicate species distributed at the American continent, whereas species distributed in two continents are represented by red tones, and those distributed in more than two continental areas in green.

In addition, we provide a first quantitative approach to determining the distribution patterns of Colombian polypores based on the assessment of 223 species (Figure 3b). Our results showed that most species are currently reported with a Neotropical distribution (34.1%), followed by Pantropical (27.1%) and Cosmopolitan (25.1%) distributions, whereas endemic species represent only 4%. However, this information may not be accurate because the taxonomic and phylogenetic concepts of many species in the group are still debated. In many cases, it has been shown that species believed to be widely distributed represent species complexes, which is a factor that contributes to substantial gaps and bias in the assessment of fungal biogeography. For instance, in recent decades, phylogenetic studies have shown that traditional genera, such as *Polyporus*, are polyphyletic, and several new genera have been segregated or reinstated since then. For example, *Polyporus udus*, originally described from Indonesia, has been widely recorded in the Neotropics. Motato-Vásquez *et al.* (2018) investigated the phylogenetic relationship of *P. udus* and its purported taxonomic synonyms in South America. This study showed that specimens from Argentina, Brazil, and Paraguay are not conspecific with Paleotropical specimens of *P. udus*. The Neotropical records are now recognised as *Bresadolia paradoxa*. There are several records of *P. udus* in Colombia, and future studies should attempt to untangle these specimens' true identity, especially because it is a species of importance as a food source for Amazonian indigenous tribes (Sanuma *et al.*, 2016).

In the same way, *Polyporus dictyopus* is a species that has been recorded as Cosmopolitan and presents a large number of heterotypic synonyms (with at least 16 known from tropical and subtropical America). Palacio *et al.* (2017) showed that at least five distinct species were hidden under *P. dictyopus*. The authors accommodated these species in two different genera, *Atroporus* and *Neodictyopus*. The study only included samples from Brazil, but *P. dictyopus* has been widely recorded from the Amazonian, Andean, and Pacific regions in Colombia. However, the identity of these specimens remains unknown.

Our compiled data show that the highest concentration of recorded polypores is in the Andes region within Colombia. This fact is not surprising since taxonomists tend to collect more intensively in the vicinity of their workplace. So, areas near important research institutions tend to show a higher concentration of species distribution records (Sobral & Stehmann, 2009). Most of the undercollected regions contain diverse habitats that are suitable for polypores, so the absence of records indicates strong sampling bias (Figure 3a). Nonetheless, sampling bias may not be the only explanation for the high diversity of polypores in the Andean region. This biome is known for its high diversity and endemism for many animals and plant taxa (Mutke *et al.*, 2014, and references therein). The high biodiversity of this biome is possibly related to its topographic and hydrologic heterogeneity, which resulted in species with narrow distribution ranges and the differentiation of small areas of endemism. Thus, the high diversity of polypores in

the Andes biome, compared with that in other Colombian biomes, may also result from the evolutionary history and geo-climatic characteristics of this biome. Currently, in Colombia, nine species of polyporeoid fungi are recognised as endemic: three of them are described from the Andean region, three from the Pacific, two from the Amazon, and one from the Caribbean. It is very premature to assess which region supports the greatest richness of endemic species with our data. For this reason, although logic indicates that we should focus on sampling poorly known places, it is important to consider that better-sampled and species-rich areas, such as the Andes biome, may still hold many undescribed and narrowly distributed species.

BIOGEOGRAPHY OF ECTOMYCORRHIZAL FUNGI IN COLOMBIA

Ectomycorrhizal (EcM) fungi present different patterns of symbiotic associations with diverse families of Angiosperms and Gymnosperms (Brundett & Tedersoo, 2018; Corrales *et al.* 2018). Owing to the obligate nature of these relationships, the occurrence of EcM fungi generally coincides with the distribution of their associated plant families, which renders plant distributions critical to understanding the biogeography and abundance of EcM fungi. However, processes of dispersal and migration in EcM fungi are not always known. Recent studies have provided data to help to elucidate apparent disjunct distribution patterns, with possible scenarios including long-distance dispersal, community migration across land bridges (with possible symbiont exchange), relictual continental disjunction and multi-hosts (Moser & Horak, 1975; Halling, 1996; Halling *et al.*, 2008; Hosaka *et al.*, 2008; Lumbsch *et al.*, 2008; Matheny *et al.*, 2009; Hackel *et al.*, in press).

In Colombia, the best-studied ectomycorrhizal systems are those associated with the dominant tree in Andean Mountain ranges, *Quercus humboldtii* (Fagaceae) (Vargas & Restrepo, 2020; Peña-Vanegas & Vasco-Palacios, 2019). There is another Fagaceae that forms monodominant EcM systems, *Trigonobalanus excelsa*, but this species is poorly studied (Peña-Vanegas & Vasco-Palacios, 2019). In the Amazonian region in Colombia, studies have been carried out on the diversity of EcM fungi associated with the host tree *Pseudomonotes tropenbosii* (Dipterocarpaceae) and the Fabaceae hosts *Aldina* sp. and *Dicymbe uaiparuensis* (Vasco-Palacios *et al.*, 2018; Peña-Vanegas & Vasco-Palacios, 2019). Most of the research on EcM fungi in Colombia has focused on inventories in few localities in the Andean and Amazon regions, so we do not know the total distribution, biology, or ecology of EcM species in the country (Chapter 4).

A total of 207 species of EcM fungi are known for Colombia. Of those, 56 are new species described from Colombian specimens, including 36 putative endemics, representing a rate of endemism of nearly 18% (Table 1, Figure 4 a–f). Most of these species are associated with Fagaceae in the Andean region of the country (43 species), and about 55% of these new species are endemic (24 species) to the country. Most of these endemic species are known only from

TABLE 1. Data about new species of EcM fungi described from Colombian specimens based on their hosts, including the total of endemic species. Biogeographic regions are based on biogeographic realms (<https://ecoregions2017.appspot.com/>)

Plant hosts	Number of endemic species in Colombia	Neotropical South American species	Neotropical Central American species	Holarctic-tropical	Global
Fabaceae (e.g. <i>Dicymbe uaiparuensis</i>)	3	37	0	0	2
Dipterocarpaceae (<i>Pseudomonotes tropenbosii</i>)	4	40	0	0	1
Fagaceae (<i>Quercus</i> spp.)	25	0	33	57	12
Fabaceae (<i>Trigonobalanus excelsa</i>)	2	0	1	0	0
Non-data, tropical lowland forests	2	1	0	0	0
Total general	36	48	34	57	15

the type specimen, or, in some cases, are known just from few collections from the type locality (e.g. *Lactarius caucae* Singer, *Russula idroboi* Singer, *Boletus orquidianus* Halling). Even though mycological expeditions have been conducted in Antioquia, Boyacá, Santander, and Tolima in the past 20 years, those did not yield any additional specimens and localities for most of these endemic species (Vargas & Restrepo, 2020; Peña-Vanegas & Vasco-Palacios, 2019). It is important to consider that a large number of unidentified fungal specimens are deposited in fungal collections around of the country. For example, in the fungal collection of the Herbarium of the Universidad de Antioquia (HUA), which is the largest in the country, houses more than 12,500 specimens, of which only 49% are identified at the species level (David *et al.* 2019; Chapter 14). In addition, most of the endemic species have no associated barcode sequences that would allow corroboration of their inferred restricted distribution.

Based on the information on the distribution of the species available on GBIF (<http://www.gbif.org>), the 207 EcM species have a primarily Neotropical distribution (44%), of those 21% occur in lowland forests in South America, and 16% in mountain areas. Near one third of the species have nordic distribution (14% Nearctic-Neotropical and 12.6% holarctic-Neotropical). Regarding the EcM species hosted by Fagaceae, 18% are endemic, 37% have a Holarctic-Neotropical (17.6%) or Nearctic-Neotropical (19.6%) distribution, and only 22% are Neotropical from mountain areas. In the case of EcM fungi from tropical lowland forests, 11% are endemic, and 76.8% occur in Neotropical-South America (Figure 5A).

Quercus (Fagaceae) is an important EcM plant host with Holarctic distribution. In Costa Rica, Panama, and Colombia, oak forests are primarily found in tropical montane ecosystems. The presence of oak forests in Colombia represents the southernmost limit of the geographic distribution of *Quercus* in the Americas, with *Quercus*

humboldtii being the only species present in South America, restricted to the Serranía del Darien, a small mountain range on the border with Panama, and the Andes Mountains in Colombia (Hooghiemstra, 2006; Rangel & Avella, 2011). Floristic studies in Neotropical Central and South America show patterns similar to that of the fauna concerning the Great American Biotic Interchange (GABI), which started with the closure of the Panama Isthmus approximately 3.0 Mya (Leigh *et al.*, 2014; O’Dea *et al.*, 2016). Plant communities in montane regions of Central America and the northern portion of South America are primarily composed of lineages of either Holarctic or Austral-Antarctic origin that subsequently dispersed south- or northwards. Phylogeographically, Costa Rica and Panama are more similar to Colombia than either are to Mexico (Kappelle, 2006). *Quercus* and its associated EcM fungi migrated southwards across the Panama Isthmus during the last glaciation. The remaining populations are now geographically isolated because of the absence of cooler environments, like those from high mountains, connecting Panama and Colombia (Halling 1996; Hooghiemstra, 2006; Halling *et al.*, 2008). Regardless of the available research on Neotropical oak communities, much of the taxonomy, diversity, and biogeographic history of their associated EcM communities in Colombia remains to be explored in-depth. This lack of knowledge is even more pronounced for *Trigonobalanus excelsa*. The other two known species of *Trigonobalanus*, are from SE Asia and this Neotropical species is an example of tropical Amphipacific disjunctions (van der Hammen & Cleef, 1983). Therefore, it is very interesting to know the EcM fungi lineages associated with *T. excelsa*, which could also have a Pantropical origin, contrary to those lineages associated with *Quercus humboldtii*, which has Holarctic origins. Studies of EcM agarics and boletes from *Quercus* forests in Costa Rica and Colombia indicate genus-level affinities with the Northern Hemisphere (59% of all EcM species) rather than those from tropical lowlands



FIGURE 4. Endemic species of EcM fungi. **A** *Russula floriformis* subsp. *floriformis*, symbiont with *Quercus humboldtii*. **B** *Phylloporus fibulatus* symbiont with *Q. humboldtii*. **C** *Sarcodon rufobrunneus* associated with *Dicymbe uaiparuensis*. **D** *Gloeocantharellus uitotanus* putatively associated with *Pseudomonotes tropenbosii*. **E** *Austroboletus amazonicus* associated with *P. tropenbosii*. **G** *Ramaria chocoënsis* without information about the possible plant host. (Photographs A by Adriana Corrales; B–E by Aída Vasco-Palacios; and G by Danny Newman.)

and temperate areas in South America (22%) (Halling *et al.*, 2008) (Figure 5b). These groups also tend towards high endemism at the species level (Halling *et al.*, 2008). In Russulaceae, a highly diverse family of EcM fungi, Andean species have different biogeographical patterns compared to those occurring in lowlands in tropical South America. The association of Andean Russulaceae with northern temperate plant lineages suggested recent co-immigration with *Quercus* when the latter colonised the rising Andes during the Pleistocene (Hackel *et al.*, in press). For example, *Russula floriformis* subsp. *floriformis* and *R. floriformis* subsp. *symphoniae* were recently described as new from montane forest dominated by *Quercus* and/or *Oreomunnea* (Fagales) from Colombia and Panama, respectively (Vera *et al.*, 2021) (Figure 4a). These two subspecies' morphological and phylogenetic proximities supported their diversification due to a co-immigration, adaptation and geographic isolation of *Quercus* and their symbionts along the Isthmus of Panama

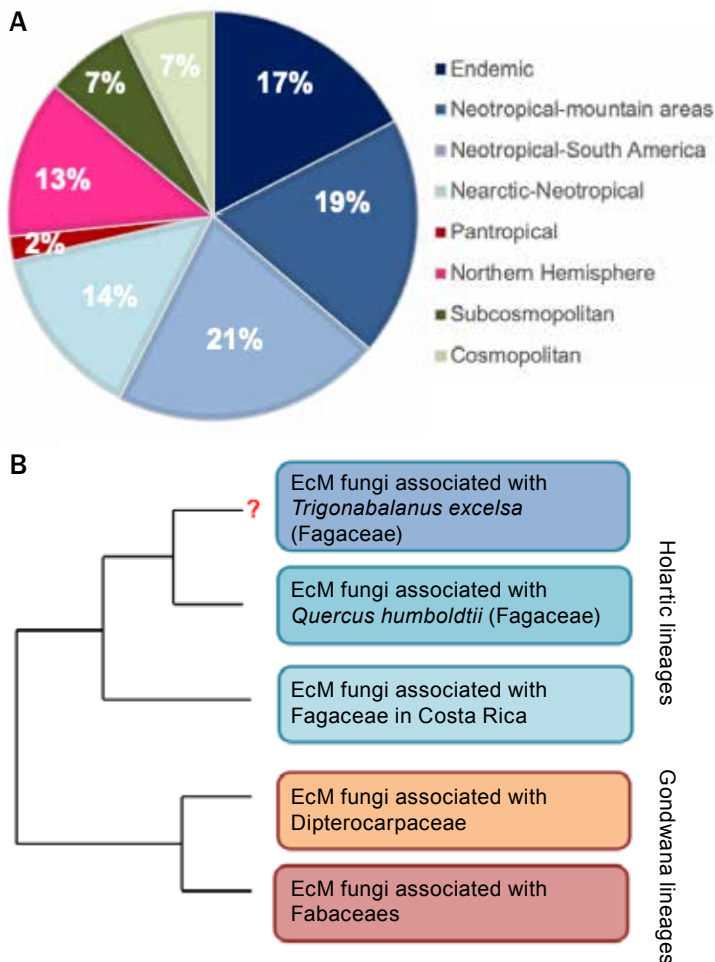


FIGURE 5. A Proportions of distribution of EcM fungi species with occurrence in Colombia, Neotropical. Blue tones indicate species distributed on the American continent, whereas red species distributed in two continents, and green are species in more than two continental areas. **B** EcM fungi in neotropical oak communities belong to Holarctic lineages. By contrast, Gondwanan lineages are represented in the EcM fungi of tropical lowland forests in the Colombian Amazon, African Fabaceae and Asian Dipterocarpaceae.

during the Pleistocene (Vera *et al.*, 2021). While there are some specific examples, in general there is a big gap in the knowledge of EcM fungi, particularly those associated with Fagaceae. For example, the EcM diversity associated with *T. excelsa* is almost unknown, and therefore we do not know whether this plant host share species of EcM fungi with *Q. humboldtii* or not, considering that they present different origins (Tropical Amphi-pacific vs Holarctic). Other little-known patterns that affect the distribution of the species is the arrival of invasive species, such as *Amanita muscaria*, which has been detected on roots of *Q. humboldtii* (Vargas *et al.*, 2019).

In wet tropical lowland forests, Dipterocarpaceae and Fabaceae represent two distantly related plant lineages within the angiosperms that have separately evolved the ability to form EcM symbioses (Wang & Qiu, 2006). As mentioned before, these hosts occur in tropical rainforests in the Amazon region, supporting a surprising diversity of EcM fungi, with a total of 114 morphospecies. However, based on the available information (descriptions or keys), only 61 of those morphospecies are correlated to species names, with 20 corresponding to species that are to science, only some of which are in process of description (Vasco-Palacios 2016; Vasco-Palacios *et al.*, 2014, 2018). Of the 61 species, 45 were associated with *Pseudomonotes tropenbosii* (Dipterocarpaceae) and 42 species with Fabaceae (Table 1). The discovery of the endemic tree *P. tropenbosii* emphasises a phylogeographical link between the Colombian Amazon and continental Africa and Madagascar (Morton *et al.*, 1999). In addition, the EcM status of *P. tropenbosii* indicates that the EcM habit evolved before the continental separation, and that radiations of EcM fungi associated with dipterocarps across continents are explained by co-migrations of the fungus and host partners (Halling *et al.*, 2008; Brearley *et al.*, 2012; Moyersoen, 2012). In addition, several EcM fungal species that were previously restricted to the Guiana Shield were extended to Central Amazonia in Colombia. For example, *Clavulina* is a cosmopolitan genus, with many species recorded growing in Fabaceae- and Cistaceae-dominated forests (Henkel *et al.*, 2012; Smith *et al.*, 2011, 2013). Uehling *et al.* (2012) proposed the Guyana region as a diversification hotspot for *Clavulina*. Eighteen species of this genus were collected from *P. tropenbosii* forests in three years of sampling, representing 72% of the total species reported from Guyana (Vasco-Palacios & Boekhout, 2022). Similarities in the EcM fungi community structure between *P. tropenbosii*, Fabaceae forests, and *Pakaraimaea* (Cistaceae) suggested a low level of host specificity. Nearly 43% of the species associated with *P. tropenbosii* have also been reported from Fabaceae forests in the Neotropics (Vasco-Palacios, 2016). This scenario is the case for the rare ascomycete, *Pseudotulostoma volvatum*, whose type specimen was collected associated with ectomycorrhizal *Dicymbe corymbosa* (Fabaceae) trees and was also found associated with *P. tropenbosii* in Colombia. Species such as *Amanita xerocybe*, *Craterellus atratus*, *Clavulina amazonensis*, and *Coltriciella oblectabilis* are widely distributed in the Amazonian region and the Guyana plateau being associated

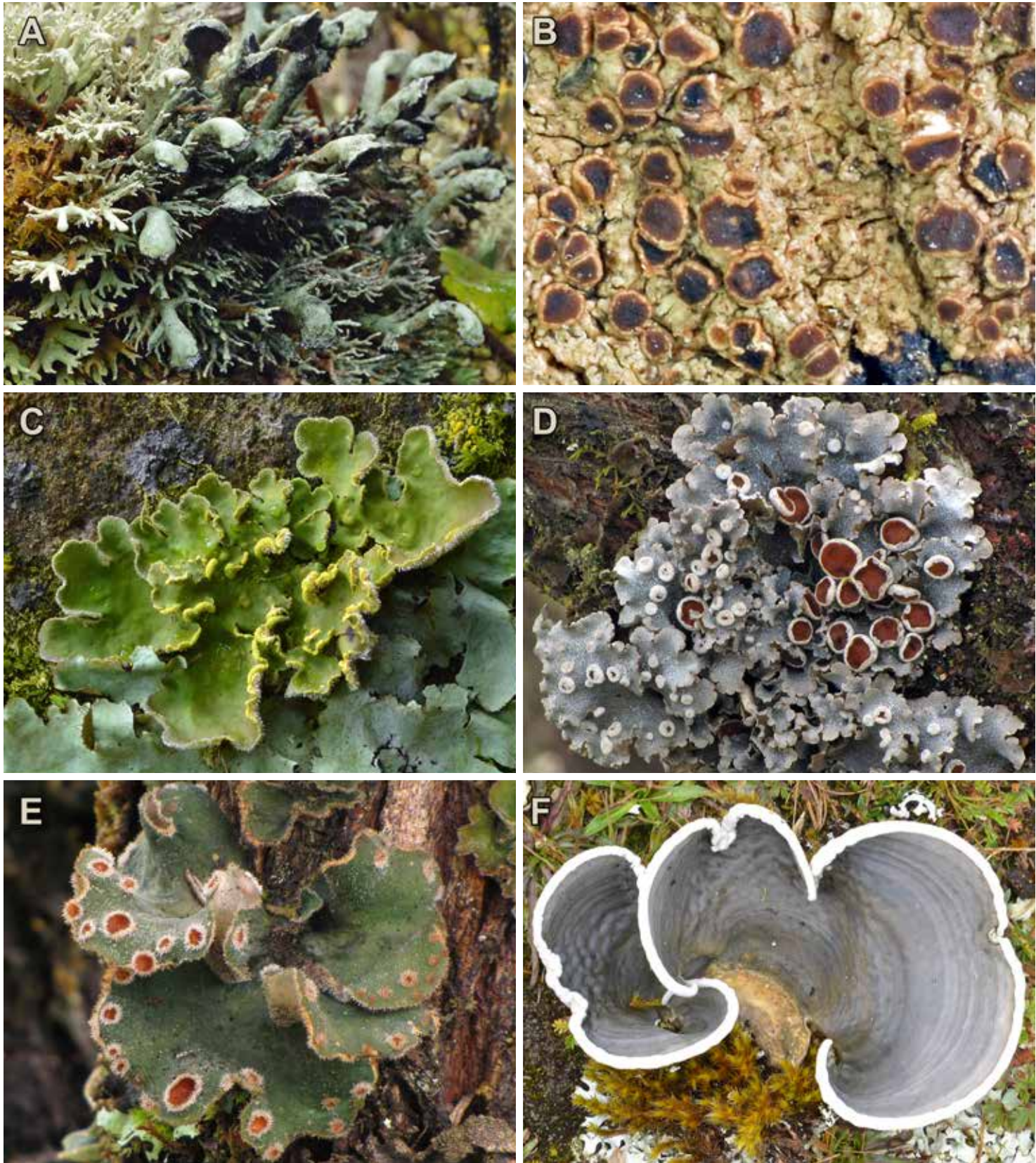


FIGURE 6. Lichenised fungi analysed in this chapter. A *Bunodophoron melanocarpum*. B *Neoprotoparmelia multifera*. C *Crocodia aurata*. D *Lobariella sipmanii*. E *Sticta hirsuta*. F *Cora elephas*. (Photographs by Robert Lücking.)

with multiple hosts (Singer *et al.*, 1983; Henkel *et al.*, 2002, 2012; Smith *et al.*, 2013; Roy *et al.*, 2016). These findings show that, although EcM symbioses seem rare in lowland tropical forests and host plants are often distributed in isolated patches, lowland forest EcM fungi may be abundant and may present broad distribution ranges.

Long-distance dispersal combined with low host specificity may increase the possibility of gene flow between geographically distant populations of these EcM fungi (Roy *et al.*, 2016; Tedersoo *et al.*, 2010; Moyersoen, 2012; Vasco-Palacios *et al.*, 2018). Other important hosts of EcM fungi in tropical lowland forests are Nyctaginaceae (e.g., *Neea*, *Guapira*) and Polygonaceae (e.g., *Coccoloba*), but little is known about these ecosystems and the role of those plant hosts in species distribution throughout the vast territory of the Amazon region (Vasco-Palacios *et al.*, 2020). Phylogenetic studies in tropical lowland EcM lineages are consistent with a Gondwanan origin, i.e., phylogeographic links between South America and Africa (Figure 5b) (Moyersoen, 2012; Hosaka *et al.*, 2008; Matheny, 2009; Koch *et al.*, 2019). Further studies will help us to identify distribution patterns of EcM fungi (dispersal vs vicariance), as well as host specificity and preferences.

BIOGEOGRAPHY OF COLOMBIAN LICHENS: TRADITIONAL TAXONOMY VERSUS MOLECULAR DATA

Chapter 6 presents an analysis of the distribution patterns of Colombian lichens, primarily relying on a phenotype-based species concept but including published results from molecular data available for some groups. According to that analysis, more than half of the species (53%) are presumably

widely distributed, including Gondwanan (American-African) and circumpacific (American-Asian) disjunctions, species found across the Northern or the Western Hemisphere, and pantropical and (sub-)cosmopolitan taxa. The largest proportion of a particular distribution type is provided by Neotropical species (35%), whereas endemic species presumably correspond only to 8.5% (Chapter 6).

To assess this pattern, we looked at eight genera for which a large amount of molecular data are available: *Bunodophoron* (Sphaerophoraceae), *Neoprotoparmelia* (Parmeliaceae), *Crocodia*, *Lobariella*, *Podostictina*, *Pseudocyphellaria*, *Sticta* (Peltigeraceae, all Ascomycota), and *Cora* (Hygrophoraceae, Basidiomycota). These lichens include crustose (*Neoprotoparmelia*), fruticose (*Bunodophoron*), and foliose lichens (all other genera; Figure 6a–f). We used the checklist published by Sipman *et al.* (2008) to assess the number of species corresponding to these eight genera in Colombia and their presumed distribution patterns before molecular studies. We then analysed published and unpublished molecular data to estimate the actual number of species in the corresponding trees and their distribution ranges (Moncada *et al.*, 2013, 2014; Lücking *et al.*, 2017a, b; Soto-Medina *et al.*, 2018; Santos *et al.*, 2019).

Based on Sipman *et al.* (2008), the eight genera correspond to 49 mostly phenotypically defined species (Table 2), with primarily broad distribution ranges: about 20% (sub-)Cosmopolitan or in the Southern Hemisphere, 10% pantropical, 12% circumpacific or in the Neotropics and Hawaii, and 2% Gondwanan (Figure 7a). By contrast, 39% were inferred as Neotropical and 12% as endemic, somewhat higher than the overall proportions for all

TABLE 2. Species corresponding to the lichenised fungal genera *Bunodophoron*, *Cora*, *Crocodia*, *Lobariella*, *Neoprotoparmelia*, *Podostictina*, *Pseudocyphellaria*, and *Sticta* in the checklist by Sipman *et al.* (2008).

Currently accepted genus	Original genus from Sipman <i>et al.</i> (2018)	Species/variety/form	Family	Distribution
<i>Bunodophoron</i>	<i>Bunodophoron</i>	<i>insigne</i>	Sphaerophoraceae	Southern Hemisphere
<i>Bunodophoron</i>	<i>Bunodophoron</i>	<i>melanocarpum</i>	Sphaerophoraceae	Cosmopolitan
<i>Cora</i>	<i>Dictyonema</i>	<i>glabratum</i>	Hygrophoraceae	Subcosmopolitan
<i>Lobariella</i>	<i>Lobariella</i>	<i>crenulata</i>	Peltigeraceae	Neotropical-Hawaii
<i>Lobariella</i>	<i>Lobariella</i>	<i>exornata</i>	Peltigeraceae	Neotropical
<i>Lobariella</i>	<i>Lobariella</i>	<i>pallida</i>	Peltigeraceae	Neotropical
<i>Lobariella</i>	<i>Lobariella</i>	<i>subexornata</i>	Peltigeraceae	Neotropical-Hawaii
<i>Neoprotoparmelia</i>	<i>Maronina</i>	<i>multifera</i>	Parmeliaceae	Circumpacific
<i>Crocodia</i>	<i>Pseudocyphellaria</i>	<i>arvidssonii</i>	Peltigeraceae	Neotropical
<i>Crocodia</i>	<i>Pseudocyphellaria</i>	<i>aurata</i>	Peltigeraceae	Pantropical
<i>Crocodia</i>	<i>Pseudocyphellaria</i>	<i>clathrata</i>	Peltigeraceae	Pantropical
<i>Pseudocyphellaria</i>	<i>Pseudocyphellaria</i>	<i>crocata</i>	Peltigeraceae	Subcosmopolitan

TABLE 2. (continued)

Currently accepted genus	Original genus from Sipman et al. (2018)	Species/variety/form	Family	Distribution
<i>Podostictina</i>	<i>Pseudocyphellaria</i>	<i>encoensis</i>	Peltigeraceae	Southern Hemisphere
<i>Pseudocyphellaria</i>	<i>Pseudocyphellaria</i>	<i>intricata</i>	Peltigeraceae	Pantropical
<i>Sticta</i>	<i>Sticta</i>	<i>ambavillaria</i>	Peltigeraceae	Gondwanan
<i>Sticta</i>	<i>Sticta</i>	<i>andensis</i>	Peltigeraceae	Neotropical
<i>Sticta</i>	<i>Sticta</i>	<i>andreana</i>	Peltigeraceae	Neotropical
<i>Sticta</i>	<i>Sticta</i>	<i>beauvoisii</i>	Peltigeraceae	Neotropical-North American
<i>Sticta</i>	<i>Sticta</i>	<i>brevior</i>	Peltigeraceae	Endemic
<i>Sticta</i>	<i>Sticta</i>	<i>canariensis</i>	Peltigeraceae	Subcosmopolitan
<i>Sticta</i>	<i>Sticta</i>	<i>cometia</i>	Peltigeraceae	Neotropical
<i>Sticta</i>	<i>Sticta</i>	<i>cordillerana</i>	Peltigeraceae	Endemic
<i>Sticta</i>	<i>Sticta</i>	<i>damicornis</i>	Peltigeraceae	Subcosmopolitan
<i>Sticta</i>	<i>Sticta</i>	<i>dilatata</i>	Peltigeraceae	Neotropical
<i>Sticta</i>	<i>Sticta</i>	<i>filicinella</i>	Peltigeraceae	Neotropical
<i>Sticta</i>	<i>Sticta</i>	<i>fuliginosa</i>	Peltigeraceae	Subcosmopolitan
<i>Sticta</i>	<i>Sticta</i>	<i>granatensis</i>	Peltigeraceae	Endemic
<i>Sticta</i>	<i>Sticta</i>	<i>gyalocarpa</i>	Peltigeraceae	Neotropical
<i>Sticta</i>	<i>Sticta</i>	<i>humboldtii</i>	Peltigeraceae	Neotropical
<i>Sticta</i>	<i>Sticta</i>	<i>impressula</i>	Peltigeraceae	Endemic
<i>Sticta</i>	<i>Sticta</i>	<i>kunthii</i>	Peltigeraceae	Neotropical
<i>Sticta</i>	<i>Sticta</i>	<i>kunthii</i> var. <i>pilosella</i>	Peltigeraceae	?
<i>Sticta</i>	<i>Sticta</i>	<i>laciniata</i>	Peltigeraceae	Neotropical
<i>Sticta</i>	<i>Sticta</i>	<i>laciniata</i> var. <i>denudata</i>	Peltigeraceae	?
<i>Sticta</i>	<i>Sticta</i>	<i>laciniata</i> var. <i>laeviuscula</i>	Peltigeraceae	?
<i>Sticta</i>	<i>Sticta</i>	<i>laevis</i>	Peltigeraceae	Neotropical
<i>Sticta</i>	<i>Sticta</i>	<i>lenormandii</i>	Peltigeraceae	Neotropical
<i>Sticta</i>	<i>Sticta</i>	<i>leucoblepharis</i>	Peltigeraceae	Neotropical
<i>Sticta</i>	<i>Sticta</i>	<i>limbata</i>	Peltigeraceae	Cosmopolitan
<i>Sticta</i>	<i>Sticta</i>	<i>macrophylla</i>	Peltigeraceae	Pantropical
<i>Sticta</i>	<i>Sticta</i>	<i>neolinita</i>	Peltigeraceae	Neotropical
<i>Sticta</i>	<i>Sticta</i>	<i>neopulmonaria</i>	Peltigeraceae	Endemic
<i>Sticta</i>	<i>Sticta</i>	<i>obvoluta</i>	Peltigeraceae	Neotropical-South American
<i>Sticta</i>	<i>Sticta</i>	<i>orizabana</i>	Peltigeraceae	Neotropical
<i>Sticta</i>	<i>Sticta</i>	<i>peltigerella</i>	Peltigeraceae	Endemic
<i>Sticta</i>	<i>Sticta</i>	<i>peruviana</i>	Peltigeraceae	Neotropical
<i>Sticta</i>	<i>Sticta</i>	<i>rudiuscula</i>	Peltigeraceae	?

TABLE 2. (continued)

Currently accepted genus	Original genus from Sipman <i>et al.</i> (2018)	Species/variety/form	Family	Distribution
<i>Sticta</i>	<i>Sticta</i>	<i>sinuosa</i>	Peltigeraceae	Circumpacific
<i>Sticta</i>	<i>Sticta</i>	<i>subcaperata</i>	Peltigeraceae	Circumpacific
<i>Sticta</i>	<i>Sticta</i>	<i>subscrobiculata</i>	Peltigeraceae	Neotropical
<i>Sticta</i>	<i>Sticta</i>	<i>tomentella</i>	Peltigeraceae	Circumpacific
<i>Sticta</i>	<i>Sticta</i>	<i>tomentosa</i>	Peltigeraceae	Pantropical
<i>Sticta</i>	<i>Sticta</i>	<i>tomentosa</i> f. <i>latior</i>	Peltigeraceae	?
<i>Sticta</i>	<i>Sticta</i>	<i>tomentosa</i> f. <i>ornata</i>	Peltigeraceae	?
<i>Sticta</i>	<i>Sticta</i>	<i>tomentosa</i> var. <i>dilatata</i>	Peltigeraceae	?
<i>Sticta</i>	<i>Sticta</i>	<i>weigeli</i>	Peltigeraceae	Subcosmopolitan

lichen fungi (see Chapter 6). However, when analysing the same genera based on molecular data, the total number of species was estimated at 283, almost six times the previous number, demonstrating the high degree of hidden diversity in these taxa. The bulk of these additional species is found in the genera *Cora* and *Sticta*, where many of the phylogenetically defined clades still await formal description (Lücking *et al.*, 2014, 2017a). When inferring the distribution of these lineages, the overwhelming majority (95%) was reconstructed as either endemic or Neotropical (Figure 7b). The exact proportion of truly endemic versus more widespread Neotropical species is difficult to assess due to the lack of dedicated inventories in many other Neotropical areas. However, it is to be expected that many of these species also occur in other South American countries, and some may extend to Central America and/or the Caribbean, so the current 75% endemic versus 20%

Neotropical species will likely shift in favour of the latter. However, the global data for these groups suggest that these species are not intercontinentally widespread.

The observed difference between traditional phenotypic and combined molecular-phenotypic species concepts in these groups is substantial, showing an entirely different picture of biogeographic patterns of Colombian lichens (Figure 7a, b). Nevertheless, it is not possible to extrapolate these results to all lichenised lineages in Colombia. The hyperdiversity of *Cora* in particular is distorting the picture due to the high degree of previously unrecognised, hidden diversity in this genus, from just one to currently 78 species recognised in Colombia. Even so, this exercise suggests that biogeographical distribution patterns derived from traditional, phenotype-based species concepts are not reliable.

CONCLUSIONS

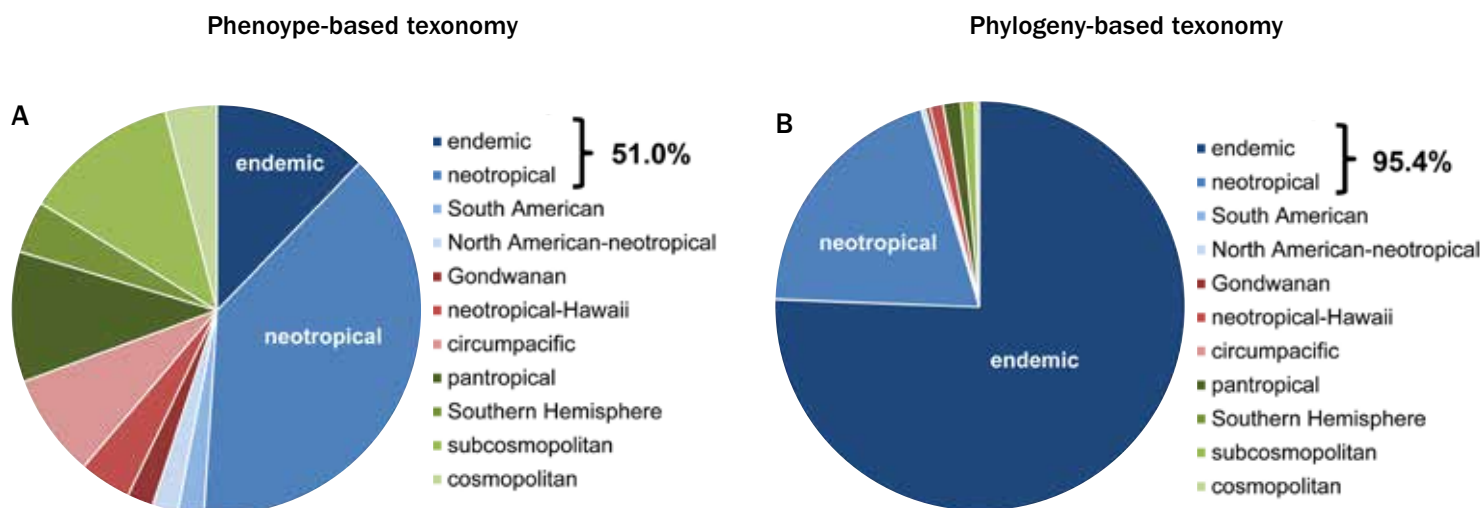


FIGURE 7. Proportions of distribution types among species of eight selected lichen-forming fungal genera in Colombia.

Our assessment of three selected groups of fungi in Colombia shows that various factors contribute to substantial gaps and bias in assessing fungal biogeography in species-rich tropical countries. One of these factors is the often poor knowledge on the ecology and distribution of species and their accurate delimitation. If these factors are not considered, biogeographical assessments can be significantly misleading, both for individual species and for fungi as a whole. This has implications for evaluating their status as potential endemics and their conservation assessment. Precise knowledge of species is one requirement to address this problem, and cataloguing all species on the planet should be the main goal of biodiversity research. However, discovering and naming species is just part of the challenge. Knowing their ecology and geographic distribution is equally important if we intend to fully understand and preserve Earth's biota. Using polypores, ectomycorrhizal fungi, and lichenised fungi as examples, we have demonstrated that species in these groups are generally poorly known, and their biogeographical patterns are hard to assess.

Therefore, fungal distribution ranges are often misrepresented by available records within and outside Colombia. Targeted field explorations, particularly in remote habitats, and phylogeographic studies are needed to provide reliable data to correct these issues. This kind of study should complement important but undervalued, continuously updated species lists and distribution reports. The maintenance and improvement of collection databases, such as ColFungi (<https://colfungi.org>), GBIF (<http://www.gbif.org>), and SIB (<https://sibcolombia.net>) will contribute to the broad distribution of knowledge about the Colombian fauna. All of these efforts require the continued work of trained taxonomists, who continue to be essential assets in the mission to document and understand Colombia's and the world's biodiversity.

Acknowledgements

We would like to thank the reviewer Manuela dal Forno for her insightful suggestions.

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Amanita xerocybe

[Aida Marcela Vasco-Palacios]



Catalogue of Fungi of Colombia

Royal
Botanic
Gardens **Kew**

Edited by
Rafael F. de Almeida
Robert Lücking
Aída Vasco-Palacios
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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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Front cover photo credit: Fungi mosaic made from photographs included in this book, based on the photograph of the species *Cyptotrama asprata* (Basidiomycota) by Nataly Gómez-Montoya. **Design cover by R.F. Almeida; back cover background photo credit:** *Ganoderma* (Mauricio Diazgranados © RBG Kew); **back cover fungi photo credits:** *Lepidostroma calocerum* (Robert Lücking ©), *Tetrapyrgos alba* (Nataly Gómez-Montoya © RBG Kew), *Pleurotus djamor* (Nataly Gómez-Montoya © RBG Kew), *Cordyceps nidus* (Robert Lücking ©), *Dacryopinax spathularia* (Kent Brothers © RBG Kew), *Cyathus striatus* (Aída Marcela Vasco-Palacios ©), *Aseroe rubra* (Nataly Gómez-Montoya © RBG Kew), *Xylaria multiplex* (Robert Lücking ©), *Phyllobaeis imbricata* (Robert Lücking ©), *Cladonia secundana* (Robert Lücking ©)

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The *Catalogue of Fungi of Colombia* is the first comprehensive listing of the known Colombian fungi. 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 (*ColFungi*). The checklist is accompanied by 15 chapters written by specialists, providing perspectives on the state of knowledge on the Colombian fungi, 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



9 781842 467909