



Pioneering a fungal inventory at Cusuco National Park, Honduras

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Abstract

Neotropical cloud forests are biologically and ecologically unique and represent a largely untapped reservoir of species new to science, particularly for understudied groups like those within the Kingdom Fungi. We conducted a three-week fungal survey within Cusuco National Park, Honduras and made 116 collections of fungi in forest habitats at 1287–2050 m a.s.l. Undescribed species are likely to be present in those collections, including members of the genera *Calostoma* (Boletales), *Chlorociboria*, *Chlorosplenium*, *Ionomidotis* (Helotiales), *Amparoina*, *Cyathus*, *Gymnopus*, *Pterula* (Agaricales), *Lactifluus* (Russulales), *Mycocitrus* (Hypocreales), *Trechispora* (Trechisporales), and *Xylaria* (Xylariales). In this paper, we discuss the contributions and impacts of mycological surveys in the Neotropics and propose the establishment of a long-term mycological inventory at Cusuco National Park—the first of its kind in northern Central America.

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Resumen extendido

Antecedentes: Los bosques nublados neotropicales son únicos tanto biológica como ecológicamente, y representan un reservorio de especies no exploradas por la ciencia, particularmente para grupos poco estudiados como el reino de hongos. Dentro de la cadena alimentaria, los hongos juegan un papel clave en el flujo de energía a través de los ecosistemas y proporcionan nutrición para muchos organismos. A pesar de esto, los estudios a largo plazo de las comunidades fúngicas son escasos, por lo que se crean brechas en nuestra comprensión de la diversidad de hongos, así como las interacciones interespecíficas e intraespecíficas en las que están involucradas. Aquí, presentamos las contribuciones y los estudios micológicos en el neotrópico y proponemos el establecimiento de un inventario micológico a largo plazo en el Parque Nacional Cusuco, el primero de su tipo en el norte de América Central.

Metódos: Durante tres semanas del verano de 2019, recolectamos hongos en el Parque Nacional Cusuco (1287–2050 m s. n. m.), un área protegida de bosque nublado en la cordillera Merendón, noroeste de Honduras. Nos hemos enfocado en tres tipos de colecciones: macrohongos productoras de cuerpos fructíferos (colectados en áreas de 10 × 10m, en cada punto de muestro dentro de los transectos) y levaduras aisladas del filoplano de diferentes plantas (aisladas de hojas recolectadas en los transectos) y los microhongos del orden Laboulbeniales en moscas ectoparásitas de murciélagos (colectados durante los muestreos de murciélagos en redes de niebla). Todas las muestras fueron enviadas a la Universidad de Purdue para su futura identificación.

Resultados: Los resultados preliminares de este muestreo son un total de 116 colectas (sin incluir levaduras del filoplano o Laboulbeniales), de los cuales 91 se han identificado a nivel de orden, 65 a nivel de género y 25 a nivel de especie. De estos, 34 colecciones fueron identificadas como *Agaricales*, seguidos por once colecciones de Helotiales y Hypocreales. Se identificaron un total de 37 géneros; los mejor representados fueron *Marasmius* (10 colecciones), *Xylaria* (7) y *Amanita* (4). Hasta la fecha, generamos y analizamos secuencias de la región ITS para un total

de 17 colecciones. Al realizar un BLAST en NCBI GenBank, diez secuencias compartieron entre 89.05 y un máximo de 97.60% de identidad con secuencias conocidas. Estos resultados indican que esas colecciones representan especies no descritas o especies conocidas no secuenciadas para esta región de ADN. Los géneros con especies potencialmente no descritas son: *Calostoma* (Boletales), *Chlorociboria*, *Chlorosplenium*, *Ionomidotis* (Helotiales), *Amparoina*, *Cyathus*, *Gymnopus*, *Pterula* (Agaricales), *Lactifluus* (Russulales), *Mycocitrus* (Hypocreales), *Trechispora* (Trechisporales) y *Xylaria* (Xylariales).

Discusión: Dada la escasez de colecciones de hongos de bosques nubosos, la presencia de organismos microendémicos en el Parque Nacional Cusuco y los resultados preliminares descritos aquí, es probable que numerosas nuevas especies de hongos estén esperando ser descubiertas en esta área. Por este motivo, se iniciará un proyecto de largo plazo de muestreo de hongos en el Parque Nacional Cusuco con el objetivo de describir la diversidad de hongos (macrohongos, hongos del filoplano y aquellos asociados con artrópodos) con base en la información morfológica, ecológica y molecular. Las alarmantes tasas de destrucción del hábitat son una de las principales amenazas del Parque Nacional Cusuco, por lo que existe una necesidad urgente de recolectar y documentar estas especies de hongos, especialmente las potencialmente endémicas—antes de que desaparezcan—. El estudio a largo plazo de los hongos del parque permitirá examinar las tendencias temporales en las comunidades fúngicas en relación con la variabilidad climatológica y la creciente perturbación ambiental. Así como los proyectos multidisciplinarios de Operation Wallacea también permitirán determinar qué tan bien se correlacionan las tendencias demográficas en las comunidades fúngicas con otros taxones, otra vía de investigación que en este momento sigue siendo poco explorada a escala global.

Introduction

The Kingdom Fungi includes a highly diverse group of organisms, in terms of both species richness as well as the ecological roles they deliver. Their unique biological characteristics such as polarized hyphal growth, external enzymatic digestion of macromolecular nutrients, and the production of large amounts of reproductive mitotic and meiotic spores have made the fungi one of the evolutionarily most successful groups on the planet, colonizing almost every available habitat and substratum (Cannon *et al.* 2018; Sheldrake 2020). Fungi fulfil essential roles in many ecosystems, constituting three major ecological strategies (Piepenbring *et al.* 2016; Willis 2018): 1) saprotrophs, or ‘recyclers’ of the natural environment, decay dead organic material, releasing its carbon and nutrient content back into the ecosystem; 2) mutualists, such as mycobionts in lichens, mycorrhizal fungi, and ruminant gut fungi derive their nutrients from other living organisms while providing benefits to their host, and 3) parasites and pathogens, or ‘regulators’ of the natural environment, obtain their nutrients from other living organisms and are essential in controlling host populations and maintaining biodiversity (Connell 1971).

Fungi are an important component of the food chain in terrestrial ecosystems, being a factor in the flux of energy through ecosystems and providing nutrition for many different animals—vertebrates (e.g., bonobos, tortoises, potoroos) as well as invertebrates (collembolans, mites, nematodes) (Fogel & Trappe 1978; Claridge *et al.* 1996, 1997; Verbeken 2002). For at least the past 5,000 years (Peintner *et al.* 1998), mushrooms have been used by humans for their nutritive and medicinal properties (Dong *et al.* 2015; Du *et al.* 2015; Zhang *et al.* 2015; Jumbam *et al.* 2019). Species in the genera *Agaricus*, *Ganoderma*, *Hericium*, and *Lentinula* are among the most popular ones, and are both collected by professional and amateur mycologists and domesticated and cultivated in mushroom farms around the world. Some of the most prized mushroom in genera such as *Boletus*, *Cantharellus*, *Morchella*, and *Tuber*—this last containing the most expensive food items in the world (Luard 2006; Patel *et al.* 2017)—form ectomycorrhizal associations and are hard to grow in

axenic culture. We depend on fungi and the metabolites they produce in the pharmaceutical world (e.g., penicillin, cyclosporine) and in the food industry (e.g., alcohol, citric acid). On the other hand, fungi are the cause of devastating infectious diseases (e.g., *Batrachochytrium dendrobatidis* in amphibians, *Cryphonectria parasitica* in chestnut trees, *Pseudogymnoascus destructans* in bats, *Puccinia graminis* in wheat; Leonard & Szabo 2005; Warnecke *et al.* 2012; Rigling & Prospero 2018; Scheele *et al.* 2019; Fisher & Garner 2020), of food spoilage (Pitt & Hocking 2009), and of human infections, particularly in immunocompromised patients (Sharma *et al.* 2014; Ioannou *et al.* 2019).

Apart from Arthropoda, fungi constitute the most diverse group of eukaryotes on the planet. Since the start of modern fungal taxonomy with Micheli’s (1729) *Nova Plantarum Genera*, 148,000 species have been formally described (Hibbett *et al.* 2016; Cheek *et al.* 2020). The number of described species has increased from 1,000–1,500 per year about 10 years ago to 2,073 species in 2019 (Cheek *et al.* 2020). These numbers may seem startling but are only a fraction of the estimated number of species, which ranges from a conservative 1.5 million (Hawksworth 1991) to 6.0 million species (Taylor *et al.* 2006) or more. While we are getting close to knowing all species in groups such as the flowering plants and birds, the gap between numbers of described and estimated species is huge for fungi and insects, where the bulk of species is still undescribed as of today (Mora *et al.* 2011; Hawksworth 2017). Alliances like the International Barcode of Life (<http://ibol.org/>; Adamowicz 2005) try to fill this gap, e.g., with multi-million-dollar funded programs aimed at generating DNA barcodes for hundreds of thousands of species (Hobern & Hebert 2019). The fact that the knowledge of fungi lags in comparison to most other groups of organisms can be explained by a number of factors: many fungi are microorganisms occupying ecological niches in very specialized substrates or habitats. Another important reason is that many areas, which are often hotspots for fungal diversity, remain underexplored. And it is here that tropical mycology comes in the picture. In tropical and subtropical areas, the diversity of biotic and abiotic

factors, including high density and diversity of potential host species, high humidity, and the availability of a plethora of microhabitats, might be expected to promote high fungal diversity.

Distributions of macroorganisms typically follow a latitudinal gradient wherein their diversity is negatively linked to increasing latitude (Hillebrand 2004; Mannion *et al.* 2014). In contrast, distributions of microorganisms, such as the fungi, which produce propagules that are microscopic in size, are often perceived as cosmopolitan (De Wit & Bouvier 2006), although lack of data from tropical regions has not allowed for rigorous testing of this hypothesis. A recent study based on environmental DNA from hundreds of soil samples from around the world found that diversity of both saprotrophic and parasitic soil fungi was highest in the tropics; signatures of endemism were also highest in the tropics (Tedersoo *et al.* 2014). In other words, the latitudinal gradient model is a better fit for patterns of fungal diversity. One exception noted by the authors concerns the guild of ectomycorrhizal fungi—those that are mutual associates with specific woody trees—where diversity increased towards temperate and boreal ecosystems. These results, however, may be more reflective of depauperate sampling of ectomycorrhizal fungi in tropical systems than of true trends; for example, where ectomycorrhizal communities have been studied in depth in tropical systems, species richness equals or exceeds that in most temperate systems (Smith *et al.* 2011).

To date, most fungi have been described by European and North American mycologists. This bias is reflected in type localities of described species. For example, 85% of genera of Leotiomycetes are based on a species described from temperate Europe and to a lesser extent North America (Johnston *et al.* 2019; MyCoPortal 2020); only 5% are based on species described from tropical areas, the eastern Palearctic, or the temperate Southern Hemisphere, with the fewest descriptions from Africa. The total number of type collections from the African continent is 15 in a class of over 6,000 species. As a further indicator of this temperate ecosystem bias, from 2,189 fungal species described in 2017, only 12% originated from the Neotropics and only 4% from Africa (Niskanen *et al.* 2018), whereas Europe and Asia accounted for 25% and 35%,

respectively. This clearly illustrates the major gap in our knowledge of tropical and subtropical fungi (Aime & Brearley 2012), while knowledge of tropical diversity is absolutely necessary in order to gain a complete picture of phylogeny and evolutionary history. E.J.H. Corner, botanist and mycologist at the Singapore Botanical Gardens, commented in 1946 on botanists' ignorance of the true variety of tropical forests and later stated that "mycology would be nothing without the tropics."

The exploration of tropical biodiversity and including tropical sampling in our datasets has often drastically changed our perspective on evolutionary relationships. This can be illustrated with the inclusion of mainly tropical African and Asian species in phylogenetic analyses of Russulaceae, one of the dominant ectomycorrhizal groups in all ecosystems worldwide. Whereas the largest genus, *Russula*, is hypothesized to have a Northern Hemisphere origin (Buyck *et al.* 2020), *Lactifluus* (one of the milkcap genera) is a primarily tropical genus likely of African origin, from where it radiated to different continents (De Crop 2016; De Crop *et al.* 2017). Understanding the evolution of Russulaceae in function of climate and available host trees, is only possible if tropical representatives are included. As stated before, many taxa in tropical areas (at the level of species, but also at higher taxonomic levels) are endemic and represent key factors in our evolutionary reconstructions. The exploration of ectomycorrhizal diversity in the Neotropics is in urgent need. Many groups (such as *Lactifluus*) are now relatively well-studied in tropical Africa and southeastern Asia, but it is only since the turn of the 21st century that neotropical hotspots such as the Guiana Shield and the Brazilian Amazon have received more attention.

Humans have been classifying organisms since antiquity (Lennox 1980), with the Linnaean taxonomic system having been in place for over 250 years (Linnaeus 1758). Nevertheless, the coverage of many taxonomic groups by this system is nowhere near complete (Brito 2010)—including the fungi, particularly tropical ones. There is no such thing as an inventory of tropical fungi. In fact, only a few historic initiatives were undertaken documenting neotropical fungal diversity. These generally covered

either specific groups of fungi or limited geographic ranges (e.g., Guevara & Dirzo 1998; Pérez & Camino 2000; Henkel *et al.* 2002; Chaverri & Vilchez 2006; Baroni *et al.* 2009; Piepenbring *et al.* 2011). A proposal for an All-Taxa Biodiversity Inventory (ATBI) of fungi at the Area de Conservación Guanacaste in Costa Rica, sparked by a ten-day workshop, demonstrates the enormous effort necessary just to compile a complete inventory of recorded species (Rossman *et al.* 1998). The authors reported a total of 1,200 known fungal taxa in Costa Rica (data from BPI).

One of the limitations of fieldwork is seasonal fruiting phenology of most macrofungi. Although macrofungi are present year-round as visibly undetectable microorganisms within the substrate, they are only visible, e.g., as mushrooms, during a brief fruiting period that is induced by genetic and environmental factors, such as rain. As an example, a 21-year study in a single plot in a temperate forest found that the above-ground fungal diversity was very different from what is “hidden away” in the substrate (soil, dead wood, inside living tissue, etc.) (Straatsma *et al.* 2001). Of a total of 408 recorded species in this study, only 2% were annually collected, and 5% were found for the first in year 21. During fieldwork, we are limited to those groups of fungi that are forming visible ascomata and basidiomata (Buyck *et al.* 2010; De Crop *et al.* 2019; Jumbam *et al.* 2019). When understudied regions of the world, such as many remote sites in the Neotropics, are being sampled for the first time, no herbarium collections or data are available to plan on a timeline for maximizing the probability of collecting fruiting bodies.

Some of the most extensive fungal documentation in Central America in the last decade has occurred in Panama. Piepenbring (2007) compiled an annotated checklist of 1,807 fungal species in Panama based on literature data and concluded that the unveiling of fungal diversity in the country is in the pioneering phase. A large effort for long-term monitoring of fungal diversity in the country was subsequently initiated, with monthly sampling along a 500-m transect in secondary vegetation in lowland of western Panama. Piepenbring *et al.* (2012) reported 567 species of fungi and fungus-like organisms, of which two were undescribed and 19 represented new country reports. None of the simulated species estimators approached an as-

ymptote. Intriguingly, the Whittaker plot showed a steep curve with a long “right tail” accounting for 50% singletons and 18% duplicates (meaning, rarely recorded species), a hallmark for hyperdiverse and undersampled habitats (Piepenbring *et al.* 2012). We expect this to be true for most neotropical areas and argue that long-term fungal surveys are needed to document fungal species diversity and distributions of species, which may be affected by human-caused habitat destruction and global warming, as well as to fill gaps in our understanding of how fungal taxa are related to one another.

In 2019, an opportunistic fungal survey was conducted by the first author in Cusuco National Park, a 23,440-ha protected area in the Merendón range, northwestern Honduras, under the auspices of Operation Wallacea. In this paper, we present preliminary results from this inventory and lay out a roadmap towards an enduring standardized fungal inventory in this area as part of Operation Wallacea’s multi-taxa biodiversity monitoring and surveillance programme in Honduras (Martin *et al.* 2021).

Fungal survey in Cusuco National Park, 2019

Methods

Opportunistic surveying of fungi took place in Cusuco National Park (hereafter abbreviated as CNP, located at 15°32′31″N 88°15′49″W) between 22 June and 13 July 2019. See Martin *et al.* (2021) elsewhere in this Special Issue for a summary of habitats and environmental conditions in this area. Surveys were limited to transects and survey plots around Base Camp (1572 m a.s.l.) and Guanales (1287 m a.s.l.); one Cantiles transect was sampled as well (Mochilero Trail, c. 2050 m a.s.l.). During this survey, we focused on three types of field collections: macrofungal fruiting bodies, yeasts isolated from leaf surfaces (= phylloplane yeasts), and bat fly-associated microfungi. Above-ground, ephemeral ascomata and basidiomata of non-lichenized fungi were collected along transects and at 10 × 10m² survey

plots. Fresh specimens were photographed *in situ* and at the camp. Specimens were assigned a HONDURAS19-F collection number and their metadata were recorded, including data, specific locality, geographic coordinates (when available), substratum, and surrounding habitat notes. Tentative names were assigned to specimens based on initial morphological examination. Samples were placed in plastic containers or paper bags and transported back to camp. Rice-sized pieces of tissue or 1–6 cups/peridioles were removed from each fresh specimen and stored in 1.5 ml Eppendorf tubes prefilled with either 600 µl of Nuclei Lysis Solution (Wizard Genomic DNA Purification Kit, Promega, Madison, WI) or 400 µl of AP1 buffer + 4 µl of RNase A (100 mg/ml) (DNeasy Plant Mini Kit, Qiagen, Valencia, CA). Specimens were dried with silica gel at the camp site.

We also obtained fungal strains from various leaf surfaces collected along transects to generate data on phylloplane fungal microorganisms (Toome *et al.* 2013; Haelewaters *et al.* 2020b). Leaves were cut into $1 \times 1\text{ cm}^2$ pieces that were attached with Vaseline Petroleum Jelly to the inner lid of a Petri dish containing agar media. Cultures were maintained on potato dextrose agar (PDA, Difco, Livonia, Michigan) supplemented with chloramphenicol (1 mL L21) to limit bacterial growth. Petri dishes were monitored daily for growth of colonies, which were transferred with sterilized toothpicks in 2 ml screw-cap microcentrifuge tubes prefilled with PDA medium supplemented with chloramphenicol. After shipment to the M.C. Aime laboratory, pure cultures were streaked out and stored at 4 °C. Finally, we collected bat flies during nightly bat surveys (Medina-van Berkum *et al.* 2021). Neotropical bat flies have been reported as hosts for Laboulbeniales fungi in the genera *Gloeandromyces* and *Nycteromyces* (Haelewaters *et al.* 2021).

All collections and tubes with tissue samples were sent to PUL (Kriebel Herbarium, Purdue University, West Lafayette, USA). Specimens will be deposited at GENT, PUL, and TEFH (*sensu* Thiers continuously updated). At the molecular lab at Purdue University, DNA extractions were performed with the DNeasy Plant Mini Kit and Wizard Genomic DNA Purification Kit following the manufacturers' instructions. PCR amplification targeted the internal transcribed spacer

(ITS) of the ribosomal RNA gene (rDNA), the region proposed as the fungal DNA barcode for identification (Schoch *et al.* 2012), using primers ITS1f and ITS4 (White *et al.* 1990; Gardes & Bruns 1993). PCR conditions followed Haelewaters *et al.* (2020b).

Preliminary results

Mycological survey work at CNP has only recently been initiated and all data were preliminary at the time of writing. A total of 116 collections were made in 2019 (not including phylloplane-inhabiting microfungi or Laboulbeniales), of which 91 have been identified to order-level, 65 to genus, and 25 to species. Of these, 34 collections were identified as Agaricales, the typical mushroom-formers, followed by 11 collections of both Helotiales and Hypocreales (Table 1). A total of 37 genera were identified; best represented were *Marasmius* (10 collections), *Xylaria* (7), and *Amanita* (4). To date, we generated and analyzed ITS sequences for a total of 17 collections, submitted to NCBI GenBank under accession numbers MT571521–MT571537. When blasting in GenBank (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>), ten of our newly generated ITS sequences shared between 89.05 and maximum 97.60% identity with known sequences. Using an identity threshold of 98.5% (see discussion in Lücking *et al.* 2020), these results imply that those collections represent either undescribed species or species that are currently unsequenced for this barcode. The genera with potentially undescribed species are: *Calostoma* (Boletales), *Chlorociboria*, *Chlorosplenium*, *Ionomidotis* (Helotiales), *Cyathus*, *Gymnopus*, *Mycena*, *Pterula* (Agaricales), *Mycocitrus* (Hypocreales), *Trechispora* (Trechisporales), and *Xylaria* (Xylariales) (Table 2).

An interesting case is HONDURAS-F017, our single collection of a *Lactifluus*. Upon initial blast, our ITS sequence for HONDURAS-F017 was 100% identical to *Lactifluus deceptivus* (KR364101, De Crop *et al.* 2016). However, recent phylogenetic analysis revealed that this taxon is a complex of multiple species (Delgat *et al.* 2019); blasting against the ex-lectotype sequence of *L. deceptivus* (GenBank accession number MN251093) only resulted in a 96.47% match. In

their recent paper, Delgat *et al.* (2019) described several new species in the *L. deceptivus* complex. Among them is *L. domingensis*, with which the sequence of our Honduran collection shares 99.16% identity (Table 2). A simple ITS tree (based on RAxML, Stamatakis 2014) showed that the Honduran collection in fact represents an undescribed sister species of *L. domingensis*.

Discussion

Hawksworth & Lücking (2017) stipulated that “about 85,000 of the currently accepted fungal species have no sequence data available.” In other words, for 57% of described species, no DNA sequences have been generated (Cheek *et al.* 2020). It is possible that potentially new taxa based on barcode divergence may be representative of those species for which no sequence data exist. On the other hand, a number of studies have highlighted high degrees of fungal endemism in tropical cloud forest ecosystems, such as the one sampled in this study (Lodge *et al.* 2008; Smith *et al.* 2013; Bandala *et al.* 2016). Del Olmo-Ruiz *et al.* (2017) evaluated fungal diversity and patterns of endemism in Neotropical montane cloud forests. The authors found that there is little overlap in species of fungi reported from Mesoamerica (*sensu* Myers *et al.* 2000), the Caribbean, and South America and that fungal species richness was highest in Mesoamerican cloud forests. The same authors also built a Mexican dataset and identified three regions of endemism supported by parsimony and Bayesian approaches. As a result, Del Olmo-Rui *et al.* (2017) suggested that thousands of undescribed species inhabit tropical montane cloud forests, some with very restricted distributions and potentially in danger of disappearing. Likewise, limited sampling on the remote highest peak of the Maya Mountains in Belize, known as Doyle’s Delight, a lower montane subtropical cloud forest, has led to the discovery of numerous new fungal species and genera (e.g., Baroni *et al.* 2007, 2008, 2009; Ortiz-Santana *et al.* 2007; Lodge *et al.* 2008; Ginns *et al.* 2010; Lindner *et al.* 2011; Ovrebo *et al.* 2011; Niveiro *et al.* 2020). With regard to our sequence data, given the reported high levels of fungal endemism from these habitats,

we predict that many undescribed species are to be discovered at CNP (Table 2).

Starting in 2022, a more formal fungal ATBI project will be initiated at CNP. The goals of this monitoring initiative are to describe the diversity of fungi encountered in the park based on morphological, ecological, and molecular information; and to assess potential changes in fungal abundance and fungal species diversity over multiple years. This formal survey work will consist of systematic searches on Operation Wallacea’s existing network of transects and habitat plots in CNP (details in Martin *et al.* 2021). Two transects per camp will be surveyed, with four randomly selected 10×10m survey plots that are located on each transect. On each survey plot two random subplots of 2×2m will be chosen, with 30 minutes of intensive sampling per subplot being conducted. Each subplot sampling event will be followed by processing of collections, which includes taking notes, sorting specimens, taking tissue for DNA, et cetera. Subplots will be located adjacent to the existing multi-taxa composite habitat plots along the transects, which are also being monitored for environmental variables, to characterize the soil, epiphyte density, number of samplings, and overall vegetation density. In this way, our survey methods will allow collection of not just distribution data, but comparative data on fungal diversity variation among habitats, which environmental variables define these variations, how fungal diversity changes over time, and how patterns in fungal species richness correlate with those in other surveyed taxa.

In addition to the systematic surveys targeting typical non-lichenized ascomata and basidiomata in the field, we will also collect microfungi from undersampled guilds, especially phylloplane fungi and those associated with Arthropoda. The latter includes representatives of Hypocreales and Laboulbeniales, which both remain poorly understood in the tropics (Araújo & Hughes 2016; Blackwell *et al.* 2020). For these arthropod-inhabiting fungi, mycologists will work closely with entomologists as well as mammalogists (to collect ectoparasitic flies from bats)—highlighting the inter-disciplinary collaborative approaches that we are undertaking, as per Haelewaters *et al.* (2021).

TABLE 1. Overview of macrofungal collections identified to order-, genus-, and species-level; number of genera and species identified, and number of undescribed species expected in Cusuco National Park based on the 2019 fungal survey.

Order	No. collections	Genera		Species		
		Collections	Identified	Collections	Identified	Undescribed
Agaricales	34	26	13	5	5	4
Auriculariales	1	1	1	1	1	0
Boletales	7	4	3	3	2	1
Geastrales	1	1	1	0	0	0
Helotiales	11	5	4	3	3	3
Hymenochaetales	2	2	2	2	2	0
Hypocreales	11	4	2	3	2	2
Orbiliales	3	3	1	0	0	0
Pezizales	4	3	2	0	0	0
Phallales	1	1	1	1	1	0
Polyporales	5	4	3	2	2	0
Russulales	3	3	2	1	1	1
Trechisporales	1	1	1	1	1	1
Xylariales	7	7	1	3	2	1
Totals	91	65	37	25	22	13

Long-term fungal inventory projects, such as the one here proposed, are vital for both ecological and evolutionary studies, but almost entirely lacking in the Neotropics. A pioneering 20-year survey within the Pakaraima Mountains of western Guyana, part of the lowland Guiana Shield region of South America, has documented 1,500+ species of Agaricales of which *c.* 75% are new to science (Aime *et al.* 2004), including new genera and higher lineages (Toome *et al.* 2013; Smith *et al.* 2015; Henkel *et al.* 2016, Sánchez-García *et al.* 2016; Koch *et al.* 2017); and revealed a thriving ectotrophic system estimated to carry at least 250 species of ectomycorrhizal fungi associating with a single host genus within three 1,000 m² plots of tropical lowland forest (Smith *et al.* 2011, 2017; Henkel *et al.* 2012). This is in stark contrast to the 408 total Agaricales, of which 265 were ectomycorrhizal, within the similar 21-year study in five 300 m² plots of temperate biotrophic forest (Straatsma *et al.* 2001).

As mentioned before, the inclusion of tropical taxa in our evolutionary trees has changed the way we think about taxonomic concepts, especially at the generic and family levels. For example, based on collections from the *Dicymbe*-dominated forests in Guyana, the first and only pleurotoid Catherellaceae (Henkel *et al.* 2006), craterloid and resupinate species of *Clavulina* (Thacker & Henkel 2004; Uehling *et al.* 2012), as well as the only smooth-spored species of Ganodermataceae (*Amauroderma coltricioides*) (Aime *et al.* 2003) were discovered. An extreme example, *Pseudotulostoma volvatum* is an ectomycorrhizal ascomycete that forms a stalked fruitbody with an exposed apical gleba and woody volvate base, reminiscent of *Tulostoma*, a basidiomycete (Miller *et al.* 2001; Henkel *et al.* 2006). A total of ten genera and more than 100 species have been described from the Guiana Shield to date but hundreds more are awaiting description (e.g., Aime *et al.* 2003, 2007, 2010; Matheny *et al.* 2003; Wilson *et al.* 2012; Henkel *et al.* 2014; Husbands *et al.* 2018). In other words, documenting these tropical oddities, only available through challenging fieldwork in remote areas, allows mycologists to question characters that have been traditionally used to delimit taxa and to reveal biases resulting from temperate-based concepts. Two undescribed species in the crust-like genus *Trechispora* from Guyana are quite interesting because they represent the first members of

more than fifty in the genus (He *et al.* 2019; Species Fungorum 2020) to be stipitate rather than resupinate (Fig. 1f), again broadening the taxonomic concept of a genus that has been primarily based on temperate collections (but see Larsson 1992, 1995; Ordynets *et al.* 2015). We also sampled a previously undescribed species of *Trechispora* at CNP (Figs. 1d, 1e; Table 2) that forms resupinate basidiomata with a variable hymenophore, with young irregular poroid areas and mature regions that are irpicoid to hydroid (Haelewaters *et al.* 2020a).

Conclusion

Where are the missing fungi? Hawksworth & Lücking (2017) identified three major sources for discovery of undescribed fungi – understudied habitats, cryptic species “hidden” in well-established names, and biodiversity hotspots. Neotropical cloud forests represent a rich source of undiscovered taxa in all three of these areas. The Mesoamerican biodiversity hotspot (*sensu* Myers *et al.* 2000) holds many cloud forest ecosystems, with each cloud forest ‘patch’ supporting its own unique community compositions. Cusuco National Park is a cloud forest site in Honduras that has been well studied under the umbrella of Operation Wallacea, although the fungal community has remained neglected until the initiation of this project. Given the presence of micro-endemic species within other taxa at CNP (Martin *et al.* 2021), along with the preliminary results described here, it is likely that numerous new fungal species await discovery. It may be the case that any site-restricted fungi at CNP are highly threatened with extinction given the alarming rates of habitat destruction in the Park (Hansen *et al.* 2013, 2020; Hoskins 2019). Thus, there is an urgent need to collect and document these species before they disappear. The data generated from the project will be used in educational and scientific products, informing on conservation strategies (Rossman *et al.* 1998); a priority that extends to other Mesoamerican cloud forest ecosystems that are often under heavy environmental pressures (Cayuela *et al.* 2006; Magrin *et al.* 2014).

TABLE 2. Collections from Cusuco National Park identified to species level. When available, BLAST results are presented of ITS sequences generated during this study. Shown are the top BLAST result along with the percentage identity and GenBank accession number, and reference in which the reported sequence was first published. New = new species to be described after morphological study and multi-locus sequencing.

Collection	ITS	Genus	Species	Top result	% identity	Acc. No.	Reference	New
HONDURAS19-F001	MT571521	<i>Gymnopus</i>	sp. 1	<i>Gymnopus androsaceus</i>	96.95%	MH857175	Vu <i>et al.</i> (2019)	X
HONDURAS19-F011	MT571522	<i>Amparoina</i>	sp. 1	<i>Amparoina heteracantha</i>	94.28%	MK309785	Na & Bau (2019)	X
HONDURAS19-F016	MT571523	<i>Trechispora</i>	sp. 1	<i>Trechispora sp. Brazil</i>	95.25%	MH290763	K.-H. Larsson, unpublished	X ^a
HONDURAS19-F017	MT571524	<i>Lactifluus</i>	sp. 1	<i>Lactifluus domingensis</i>	99.16%	KR364101	Delgat <i>et al.</i> (2019)	X
HONDURAS19-F022	N/A	<i>Xylaria</i>	cf. <i>polymorpha</i>					
HONDURAS19-F024	N/A	<i>Ophiocordyceps</i>	sp. 1					X ^b
HONDURAS19-F027	MT571525	<i>Ionomidotis</i>	sp. 1	<i>Ionomidotis fulvotogens</i>	89.05%	KY462808	H.-O. Baral & G. Marson, unpublished	X
HONDURAS19-F030	MT571526	<i>Panus</i>	<i>conchatus</i>	<i>Panus conchatus</i>	100%	MH016880	B.S. Kaminsky <i>et al.</i> , unpublished	
HONDURAS19-F031	MT571527	<i>Calostoma</i>	sp. 1	<i>Calostoma sp. MDO-2018b</i>	97.48%	MF521438	M. Deloya-Olvera <i>et al.</i> , unpublished	X
HONDURAS19-F032	MT571528	<i>Chlorosplenium</i>	sp. 1	<i>Chlorosplenium chlorea</i>	90.37%	MG553993	Haelewaters <i>et al.</i> (2018)	X
HONDURAS19-F036	MT571529	<i>Gyroporus</i>	aff. <i>subalbellus</i>	<i>Gyroporus subalbellus</i>	98.61%	EU718108	Wilson <i>et al.</i> (2011)	

HONDURAS19-F040	N/A	<i>Phallus</i>	<i>indusiatus</i>							
HONDURAS19-F047	MT571530	<i>Mycocitrus</i>	sp. 1	<i>Mycocitrus aurantium</i>	97.60%	MG022158	Loguercio Leite <i>et al.</i> (2018)	X		
HONDURAS19-F055	N/A	<i>Mycocitrus</i>	sp. 1					X ^c		
HONDURAS19-F057	N/A	<i>Trichaptum</i>	<i>biforme</i>							
HONDURAS19-F063	MT571531	<i>Xylodon</i>	<i>flaviporus</i>	<i>Xylodon flaviporus</i>	99.68%	KJ140637	Brazeo <i>et al.</i> (2014)	X		
HONDURAS19-F069	N/A	<i>Calostoma</i>	sp. 1							
HONDURAS19-F070	MT571532	<i>Chlorociboria</i>	sp. 1	<i>Chlorociboria aeruginosa</i>	92.74%	HQ604856	M.L. Berbee <i>et al.</i> , unpublished	X		
HONDURAS19-F072	MT571533	<i>Cyathus</i>	sp. 1	<i>Cyathus stercoreus</i>	96.61%	EU784193	Brock <i>et al.</i> (2009)	X		
HONDURAS19-F077	MT571534	<i>Oudemansiella</i>	cf. <i>canarii</i>	<i>Oudemansiella canarii</i>	99.07%	GQ892790	Petersen & Hughes (2010)			
HONDURAS19-F082	N/A	<i>Xylaria</i>	cf. <i>polymorpha</i>							
HONDURAS19-F086	MT571535	<i>Pterula</i>	sp. 1	<i>Pterula gracilis</i>	93.72%	MH861903	Vu <i>et al.</i> (2019)	X		
HONDURAS19-F095	MT571536	<i>Xylaria</i>	sp. 1	<i>Xylaria amphithele</i>	94.78%	GU300083	Hsieh <i>et al.</i> (2010)	X		
HONDURAS19-F098	N/A	<i>Auricularia</i>	<i>auriculari-judae</i>							
HONDURAS19-F099	MT571537	<i>Favolus</i>	cf. <i>tenuiculus</i>	<i>Favolus tenuiculus</i>	98.83%	MH211695	B.S. Kaminsky <i>et al.</i> , unpublished			

^a This species was formally described during the review process of this manuscript, as *Trechispora hondurensis* (Haelewaters *et al.* 2020a).

^b We have not yet processed the ITS sequence for this collection. However, according to D.P. Hughes (pers. comm.) this species of *Ophiocordyceps* is undescribed. It was found on a weevil (Coleoptera, Curculionidae) at the Mochilero Trail of Cantiles.

^c This represents the same species as collection HONDURAS19-H047. Both collections were found in close proximity of each other and are morphologically identical.

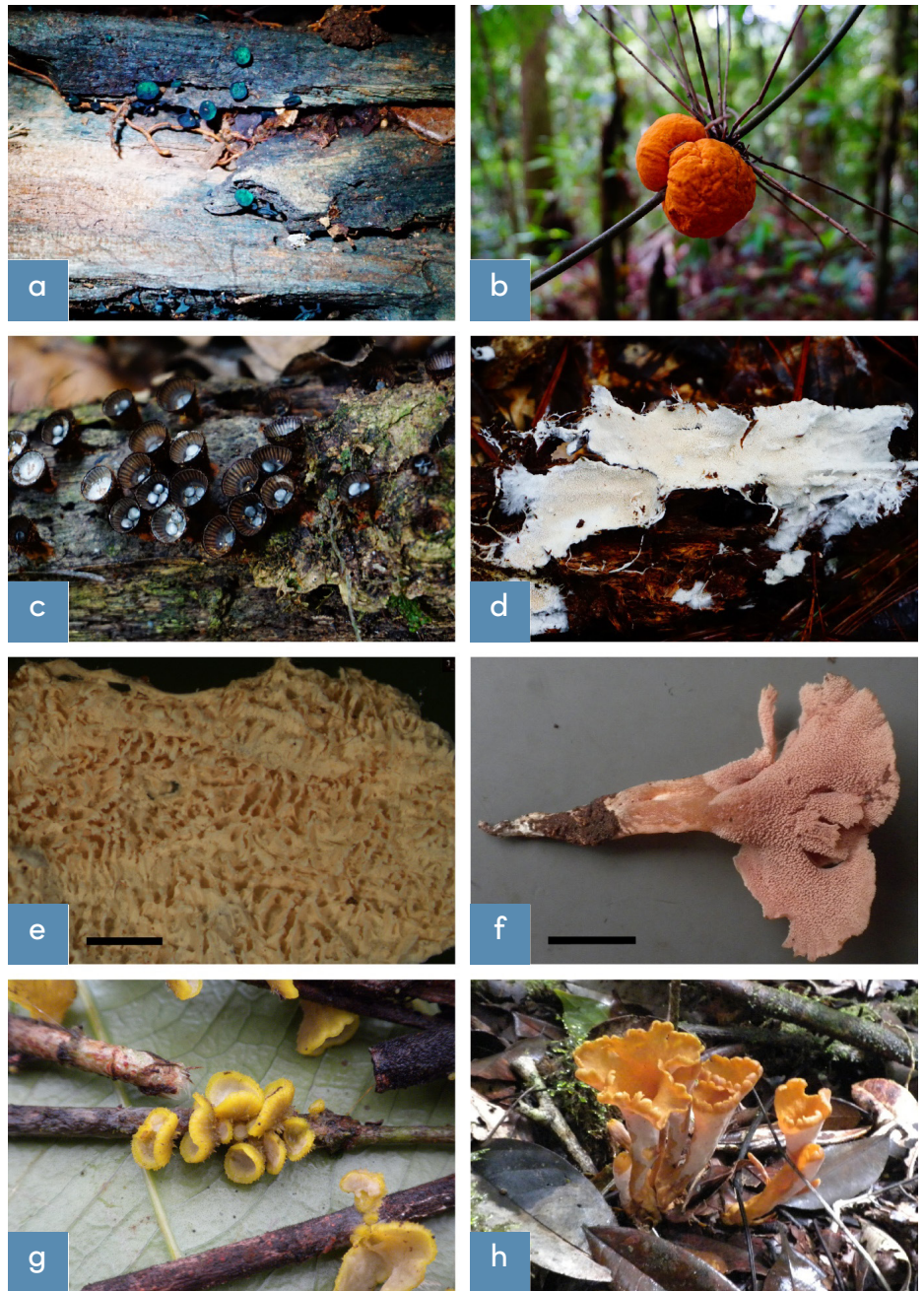


Figure 1. A variety of neotropical fungi, collected in Cusuco National Park, Honduras (a–e) and the Guiana Shield, Guyana (f–h). **a.** *Chlorociboria* sp. 1, collected at night during a mist-netting survey for bats. **b.** *Mycocitrus* sp. 1 growing on the nodes of bamboo. Unknowingly what it was in the field, we dubbed this fungus “bamboo brain”. **c.** *Cyathus* sp. 1, a bird’s nest fungus. **d–e.** *Trechispora hondurensis* [as *Trechispora* sp. 1 in Table 2], a crust-like fungus. **e.** Detail of hymenophore showing an irpicoid to hydroid area, atypical for this genus. **f.** A stipitate, undescribed species of *Trechispora*. Thus far, no stipitate representatives have been described in the genus. **g.** *Cantharellus pleurotoides*, singular in the genus for its pleurotoid basidiomata. **h.** *Clavulina craterelloides*, which could be easily mistaken for *Craterellus* based on macromorphology. Scale bars: e = 2 mm, f = 1 cm.

In addition to improving taxonomic knowledge, research in CNP will also provide novel insights into macroecological patterns, shedding further light on, for example, latitudinal diversity gradients in the Kingdom Fungi. The long-term nature of this study will allow for the examination of temporal trends in fungal communities in relation to climatological variability and increasing environmental disturbance; themes that remain poorly studied throughout the tropics. The multi-disciplinary nature of the Operation Wallacea project will also allow the determination of how well demographic trends in fungal communities correlate with those in more easily-studied taxa — another avenue of research that at this point remains poorly explored on a global scale. Finally, the initiation of this project in CNP will have the benefits of educating several hundred students from all over the world each year on the ecological importance of fungi and the methods used to survey them in the field—an opportunity that is rarely available during tropical field courses.

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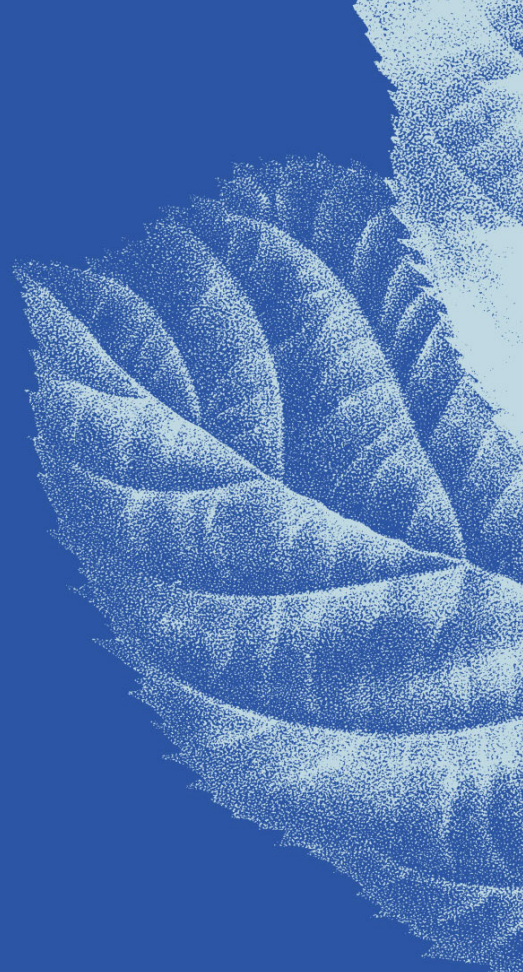
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