

UNIVERSIDAD SAN FRANCISCO DE QUITO USFQ

Colegio de Ciencias Biológicas y Ambientales

**Analysis of *Cordyceps* s.l. diversity inside Tiputini Biodiversity
Station (TBS), Ecuador.**

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Biología

Trabajo de fin de carrera presentado como requisito
para la obtención del título de
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Quito, 23 de Mayo de 2023

UNIVERSIDAD SAN FRANCISCO DE QUITO USFQ

COLEGIO DE CIENCIAS BIOLÓGICAS Y AMBIENTALES

**HOJA DE CALIFICACIÓN
DE TRABAJO DE FIN DE CARRERA**

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Station, Ecuador.

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Quito, 23 de Mayo de 2023

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RESUMEN

Los hongos *Cordyceps* s.l. parasitan a los artrópodos terrestres y otros hongos. Estos hongos entomopatógenos infectan insectos y arañas, a veces manipulan a su hospedero al cambiar su comportamiento para alcanzar una ubicación óptima, comer a su huésped, desarrollar un cuerpo fructífero desde de el cadáver y esporular para repetir el ciclo y alcanzar nuevos hospederos. Este comportamiento es único en estos hongos y su fama resulta de interés para la agroindustria como biocontrol de plagas y para la industria médica debido a sus propiedades medicinales. Este estudio tiene como objetivo describir la diversidad de *Cordyceps* s.l. encontrada en la Estación de Biodiversidad Tiputini (TBS), ubicada en lo profundo de la Amazonía ecuatoriana, un lugar conocido por su megabiodiversidad. A pesar de ser un grupo poco estudiado en Ecuador, la diversidad de *Cordyceps* s.l. en la región de Tiputini es enorme en comparación con otras regiones tropicales. Se recolectaron un total de 82 muestras que fueron identificadas morfológicamente en 32 morfoespecies. Las muestras recolectadas en este estudio presentan cuatro observaciones poco comunes. Un espécimen hospedero con 3 morfoespecies morfológicamente diferentes, un par de muestras con hiperparásitos del género *Niveomyces*, un morfo sexual de *O. humbertii* a nivel de los ojos, y un hallazgo raro de un Opiliones parasitado por *Gibellula cf. pulchra*.

Palabras clave: Cordycipitaceae, Clavicipitaceae, hongos entomopatógenos Ophiocordycipitaceae, Cordyceps, Ophiocordyceps, diversidad, taxonomía.

ABSTRACT

The fungi group *Cordyceps* s.l. parasitize on land arthropods and other fungi. These entomopathogenic fungi infect insects and spiders, sometimes manipulating their host by changing their behavior to reach an optimal location, eat their host, grow a fruiting body out of its corpse and sporulate to repeat the cycle and reach new hosts. Such behavior is unique to these fungi and their fame is of interest to the agroindustry as pest biocontrol and to the medical industry because of its medicinal properties. This study aims to describe the *Cordyceps* s.l. diversity found on Tiputini Biodiversity Station (TBS) located in the deep Ecuadorian Amazon, a known place for its megabiodiversity. Although it is an understudied group in Ecuador, the *Cordyceps* s.l. diversity in the Tiputini region is huge compared to other tropical regions. A total of 82 samples were collected and morphologically identified into 32 morphospecies. The collected samples in this study show four rare observations. One host specimen with 3 morphologically different morphospecies, a couple of samples with hyperparasites of the *Niveomyces* genus, one sexual morph of *O. humbertii* at eye level, and a rare finding of an Opiliones being parasitized by *Gibellula* cf. *pulchra*.

Key words: Cordycipitaceae, Clavicipitaceae, entomopathogenic fungi, Ophiocordycipitaceae, Cordyceps, Ophiocordyceps, diversity, taxonomy

TABLE OF CONTENTS

<i>Introduction</i>	10
<i>Materials and methods</i>	12
Area of study	12
Field collections	12
Morphological observations.....	13
<i>Results</i>	14
Taxonomy	16
<i>Conclusions</i>	31
<i>Discussion</i>	33
<i>Bibliography</i>	36
<i>Attachment A:</i>	45

TABLE INDEX

Table 1. Collected specimen information, host association and location site.	14
Table 2. Identified morphospecies and abundance	28

FIGURE INDEX

Figure 1. Trail map of Tiputini biodiversity Station.....	12
Figure 2. <i>Ophiocordyceps curculionum</i> specimens found on Tiputini Biodiversity Station...	19
Figure 3. <i>Ophiocordyceps australis</i> complex.....	22
Figure 4. Some of the collected <i>Cordyceps</i> s.l. included in this study	27

INTRODUCTION

Fungi play a big role in the nutrients cycles and are known as the master decomposers of dead organic matter, returning it as nutrients to the soil, especially in highly dynamic Amazonian soils (T. Sanjuan et al., 2001; Shang et al., 2015). But not all of the fungi feed on the dead. The entomopathogenic fungi *Cordyceps* s.l. (Hypocreales) are famous for their ability to infect living insects, spiders or even other truffle-like fungi of the genus *Elaphomyces* (Mains, 1947, 1958). They possess a high host specificity with the ability to influence on ecological communities as a biocontrol agent (Araújo et al., 2015, 2020; Lin et al., 2020; T. Sanjuan et al., 2001). Some of these fungi, like the *Ophiocordyceps unilateralis* complex can manipulate the behavior of carpenter ants chemically and mechanically (Shang et al., 2015), in such a way that the fungus obligates their ant host to reach death locations optimal for spore dispersion (Andersen et al., 2009). This characteristic extended phenotype has earned them the name of “Zombie-ant fungus”. Each cordyceps (= *Cordyceps* s.l.) species has a fairly defined range of hosts it can infect that embraces eight orders of arthropods such as Hemiptera, Lepidoptera, Coleoptera, Hymenoptera, Diptera, Dermaptera, Araneae and Orthoptera (Mongkolsamrit et al., 2020; Nikoh & Fukatsu, 2000).

The cordyceps group is not monophyletic and comprises around 1300 known species within three families: Cordycipitaceae, Clavicipitaceae and Ophiocordycipitaceae (Ascomycota) (Dong et al., 2022; Shrestha et al., 2017; Zha et al., 2018). These fungi are endoparasites that reproduce through sexual (ascospores) or asexual (conidia) spores (Mora et al., 2018). The host is recognized upon adhesion of the fungal spore and formation of the appressoria that penetrates the cuticle. It then starts to replicate with yeast-like cells inside the hemocoel of the insect and either develops mycosis to produce asexual conidial spores or colonizes the whole insect to form a fruiting body that, once mature releases ascospores into the environment (Araújo & Hughes, 2016; Hughes et al., 2016; Mora et al., 2018; Shang et al., 2015). This ability is considered an extended phenotype of the parasite (Andersen et al., 2009) and has served well in the agroindustry for biological pest control (Jiang et al., 2019; Li et al., 2019; Zhao et al., 2016).

Cordyceps fungi have been traditionally used as medicine in ancient China (Zha et al., 2018). The market around the consumption of *Ophiocordyceps sinensis* can reach values of \$32,000 (USD) per kg for top quality in late 2006 (Winkler, 2008). Thanks to new research stating the beneficial compounds this tradition has developed new interests on western natural medicine culture. Amongst the most studied medicinal compounds are cordycepin, adenosine, polysaccharides and carotenoids, all with anti-tumor properties on *O. sinensis* and *C. militaris* (Liu et al., 2015; Lou et al., 2019) and anticancer cordycepin analogue isolated from *C. militaris* used in phase I clinical trials (Schwenzer et al., 2021). Traditional consumption of cordyceps has been limited to specific regions in Asia (Liu et al., 2015), where cordyceps diversity is relatively low compared to the neotropics (T. I. Sanjuan et al., 2015). Cordyceps consumption in South America is nearly non-existent. Only one report of traditional

consumption of *Ophiocordyceps melolonthae* as food in the Ecuadorian amazon (Gamboa, 2019).

Some of the first diversity studies of entomopathogenic fungi in South America date back to the beginnings of the 20th century and include the description of *Isaria pistillarieformis* Patouillard and *Cordyceps witii* Hennings with Ecuadorian specimens, later known as the asexual stage of *Cordyceps clavulata* Schwein and *Cordyceps caloceroides* Berk. & M.A. Curtis respectively (Petch, 1932). Nowadays most descriptions of new cordyceps species include specimens from the west amazon basin (Araújo et al., 2015, 2020; Evans, 1982; Evans & Samson, 1984; T. I. Sanjuan et al., 2015), southeast Asia (Aini et al., 2020; Mongkolsamrit et al., 2020), Japan (Araujo et al., 2020; Araújo et al., 2021) and China (Dong et al., 2022; Shrestha et al., 2019). Although many collections include specimens from Ecuador, few describe the diversity composition of cordyceps in the country.

The Tiputini region inside the Yasuni National Park is one of the most biodiverse regions on earth, a hotspot for fauna and flora diversity (Bass et al., 2010). Nevertheless, little is known about the fungal diversity in this area, even less for cordyceps fungi. The last reports of new species in this area are based on collections from 2004 with the description of *Ophiocordyceps tiputini* T. Sanjuan & R.M. Kepler and *Cordyceps diapheromeriphila* T. Sanjuan & S. Restrepo (Sanjuan et al., 2014; Sanjuan et al., 2015). Because of the richness and diversity of entomofauna in the amazon basin, there is plenty of room for a vast speciation for entomopathogenic fungi. It is of great importance to understand the composition of cordyceps species in Tiputini, since it represents one of the most endangered territories threatened by oil and mining industry expansion (Bass et al., 2010). A better understanding of these fungi can open up perspectives on their ecological role in population control (Sanjuan et al., 2015), host manipulation mechanisms (Shang et al., 2015), host-parasite co-evolution (Tian et al., 2010) and genetic resources.

It is only a matter of increasing research efforts and fomenting mycological studies in Ecuadorian academy to achieve new findings and profit from the vast undiscovered species that reside this mega-biodiverse country. This study describes the diversity and composition of cordyceps fungi inside Tiputini Biodiversity Station during a 10-day excursion from May to June 2022.

MATERIALS AND METHODS

Area of study

Sampling was carried along the trails inside the Tiputini Biodiversity Station (TBS) located on the shores of the Tiputini river which is colliding with the National Park Yasuni, in the Orellana province (0.6384694° S, 76.1490806° W).

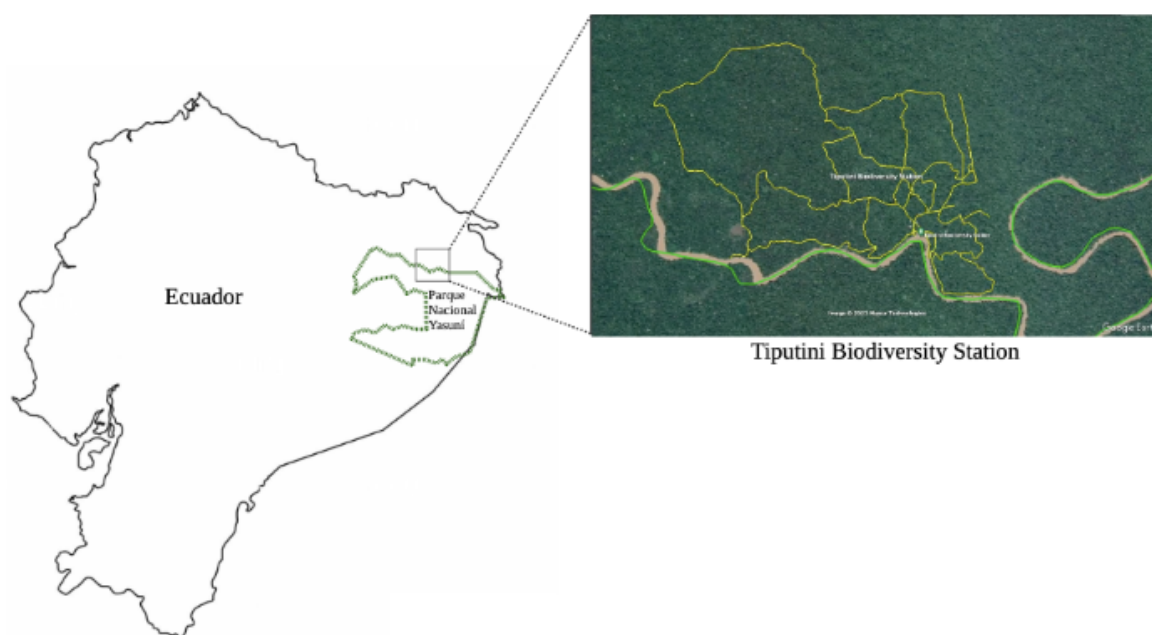


Figure 1. Trail map of Tiputini biodiversity Station

On the map shown in Figure 1, the yellow lines show the different trails that compose TBS and the Yasuni National Park border is shown with the green line.

TBS is composed of terra-firme and varzea forest types with hilly terrain and lowlands that flood during rainy season. Only one sample was collected in the river port of Estación Científica Yasuní (ECY) (0.674358° S; 76.39736° W) upon arrival.

Field collections

The sampling protocol consisted on systematic and careful inspections of soil, tree trunks, on and under leaf litter, downed wood, elevated plant structures (<2 m), and decomposing organic matter (Araújo et al., 2015). Searching protocol consisted on 2-4 hour walks along each selected trail. A total of 8 diurnal and 4 nocturnal excursions were made, reaching a total of 52 hours per person as sampling effort.

The infected host, and the surface to which they were attached, were photographed in-situ and then collected in plastic 3-vents petri dishes and other plastic containers for bigger specimens. Whenever it was possible, collected samples were examined the same day to

avoid color and morphology deterioration. Specimens were sampled under the collection permit MAAE-ARSFC-2022-2243.

Morphological observations

For morphological identification, specimens were placed under a stereoscope for a detailed observation of stromata, perithecia, color and texture. Each sample was then compared to the best description of species of the region that matched to the ones collected. Examination of fresh macroscopic characters was based on Dong et al. (2022). Fungal fruiting bodies were examined for color descriptions, size and host identification to the extent possible allowed by the condition of the specimen. Collections were air-dried and later frozen, to avoid mold and fungi-eating mites, then stored in the Ecuadorian Herbarium for Economical-Botany (QUSF). Additional material provided by the QCA Herbarium of the Pontificia Universidad Católica (PUCE) was revised for comparison.

No microscopic structures were observed, neither agar cultures were made due to complications with temperature melting the agar and the lack of a sterile workplace in such a remote place inside the Amazon. For that reason, tissue samples were collected to focus on molecular identification to compensate the lack of microscopical data.

The molecular work is still pending. The DNA was already extracted out of the tissue samples and are frozen in the Plant Biotechnology Laboratory of Universidad San Francisco de Quito (USFQ). All set to be amplified with PCR using the ITS4 and ITS5 primers, and eventually sequenced for molecular identification.

RESULTS

A total of 82 samples of entomopathogenic fungi were collected along the different trails of TBS, with an exception of sample COR01 that was found and collected beside the river port of ECY, which are listed on Table 1. Hosts with samples COR14 and COR37 presented perithecia with morphological differences within each host and for that reason, the different morphospecies (COR14A, COR14B, COR14C, COR37A and COR37B) were categorized as additional specimens, which adds to a total of 85 samples.

Of all collected specimens, 67 samples (78,82%) belong to the Ophiocordycipitaceae family, 20 to the Cordycipitaceae (20%) and only one sample belongs to the Clavicipitaceae family (1,18%).

Table 1. Collected specimen information, host association and location site.

Voucher no.	Taxon	Code	Host	Trail
QUSF-F 1	<i>Hymenostilbe</i> sp.	COR01	Diptera	ECY harbor
QUSF-F 2	<i>Ophiocordyceps australis</i>	COR02	Formicidae	Chichico
QUSF-F 3	<i>O. australis</i>	COR07	Formicidae	Harpía
QUSF-F 4	<i>O. australis</i>	COR15	Formicidae	TBS dining hall
QUSF-F 5	<i>O. australis</i>	COR16	Formicidae	Chichico
QUSF-F 6	<i>O. australis</i>	COR17	Formicidae	Chichico
QUSF-F 7	<i>O. australis</i>	COR18	Formicidae	Chichico
QUSF-F 8	<i>O. australis</i>	COR22	Formicidae	Harpía
QUSF-F 9	<i>O. australis</i>	COR26	Formicidae	Lago
QUSF-F 10	<i>O. australis</i>	COR51	Formicidae	Chorongo
QUSF-F 11	<i>O. australis</i>	COR59	Formicidae	Chorongo
QUSF-F 12	<i>O. australis</i>	COR81	Formicidae	Lago
QUSF-F 13	<i>Ophiocordyceps nutans</i>	COR03	Pentatomidae	Numa
QUSF-F 14	<i>O. nutans</i>	COR39	Pentatomidae	Matapalo
QUSF-F 15	<i>O. nutans</i>	COR47	Pentatomidae	Matapalo
QUSF-F 16	<i>Ophiocordyceps curculionum</i>	COR06	Curculionidae	Numa
QUSF-F 17	<i>O. curculionum</i>	COR08	Curculionidae	Lab TBS
QUSF-F 18	<i>O. curculionum</i>	COR12	Curculionidae	Harpía
QUSF-F 19	<i>O. curculionum</i>	COR38	Curculionidae	Lab TBS
QUSF-F 20	<i>Ophiocordyceps</i> cf. <i>curculionum</i>	COR04	<i>Pselaphacus nigropunctatus</i>	Matapalo
QUSF-F 21	<i>Ophiocordyceps engleriana</i>	COR05	Araneae	Matapalo
QUSF-F 22	<i>Ophiocordyceps kniphofioides</i>	COR09	Formicidae	Harpía
QUSF-F 23	<i>Ophiocordyceps</i> aff. <i>kniphofioides</i>	COR11	Formicidae	Maquisapa
QUSF-F 24	<i>O. kniphofioides</i> aff.	COR37A	<i>Paraponera clavata</i>	Harpía
QUSF-F 25	<i>Ophiocordyceps</i> aff. <i>ponerianum</i>	COR14B	Formicidae	TBS dining hall
QUSF-F 26	<i>O. ponerianum</i> aff.	COR43	<i>Paraponera clavata</i>	Chorongo

QUSF-F 27	<i>Ophiocordyceps</i> aff. <i>unilateralis</i>	COR19	Formicidae	Matapalo
QUSF-F 28	<i>O. unilateralis</i> aff.	COR20	Formicidae	Matapalo
QUSF-F 29	<i>O. unilateralis</i> aff.	COR23	Formicidae	Harpía
QUSF-F 30	<i>O. unilateralis</i> aff.	COR24	Formicidae	Harpía
QUSF-F 31	<i>O. unilateralis</i> aff.	COR25	Formicidae	Harpía
QUSF-F 32	<i>O. unilateralis</i> aff.	COR29	Formicidae	Matapalo
QUSF-F 33	<i>O. unilateralis</i> aff.	COR33	Formicidae	Guacamayo
QUSF-F 34	<i>O. unilateralis</i> aff.	COR34	Formicidae	Guacamayo
QUSF-F 35	<i>O. unilateralis</i> aff.	COR35	Formicidae	Chichico
QUSF-F 36	<i>O. unilateralis</i> aff.	COR40	Formicidae	Matapalo
QUSF-F 37	<i>O. unilateralis</i> aff.	COR44	Formicidae	Matapalo
QUSF-F 38	<i>O. unilateralis</i> aff.	COR45	Formicidae	Matapalo
QUSF-F 39	<i>O. unilateralis</i> aff.	COR46	Formicidae	Matapalo
QUSF-F 40	<i>O. unilateralis</i> aff.	COR50	Formicidae	Guacamayo
QUSF-F 41	<i>O. unilateralis</i> aff.	COR52	Formicidae	Matapalo
QUSF-F 42	<i>O. unilateralis</i> aff.	COR55	Formicidae	Chorongo
QUSF-F 43	<i>O. unilateralis</i> aff.	COR56	Formicidae	Chorongo
QUSF-F 44	<i>O. unilateralis</i> aff.	COR60	Formicidae	Guacamayo
QUSF-F 45	<i>O. unilateralis</i> aff.	COR61	Formicidae	Guacamayo
QUSF-F 46	<i>O. unilateralis</i> aff.	COR62	Formicidae	Guacamayo
QUSF-F 47	<i>O. unilateralis</i> aff.	COR63	Formicidae	Guacamayo
QUSF-F 48	<i>O. unilateralis</i> aff.	COR64	Formicidae	Guacamayo
QUSF-F 49	<i>O. unilateralis</i> aff.	COR65	Formicidae	Guacamayo
QUSF-F 50	<i>O. unilateralis</i> aff.	COR66	Formicidae	Guacamayo
QUSF-F 51	<i>O. unilateralis</i> aff.	COR67	Formicidae	Guacamayo
QUSF-F 52	<i>O. unilateralis</i> aff.	COR68	Formicidae	Guacamayo
QUSF-F 53	<i>O. unilateralis</i> aff.	COR70	Formicidae	Guacamayo
QUSF-F 54	<i>O. unilateralis</i> aff.	COR78	Formicidae	Chichico
QUSF-F 55	<i>O. unilateralis</i> aff.	COR79	Formicidae	Chichico
QUSF-F 56	<i>Paraisaria amazonica</i>	COR27	Orthoptera	Mata-Mata
QUSF-F 57	<i>P. amazonica</i>	COR36	Orthoptera	Chichico
QUSF-F 58	<i>Ophiocordyceps</i> aff. <i>humbertii</i>	COR41	Vespidae	Matapalo
QUSF-F 59	<i>Ophiocordyceps lloydi</i> var. <i>Binata</i>	COR71	Formicidae	Guacamayo
QUSF-F 60	<i>O. lloydi</i> var. <i>Binata</i>	COR72	Formicidae	Guacamayo
QUSF-F 61	<i>O. lloydi</i> var. <i>Binata</i>	COR73	Formicidae	Guacamayo
QUSF-F 62	<i>Ophiocordyceps</i> sp. 1	COR14A	Formicidae	TBS dining hall
QUSF-F 63	<i>Ophiocordyceps</i> sp. 2	COR14C	Formicidae	TBS dining hall
QUSF-F 64	<i>Ophiocordyceps</i> sp. 3	COR32	<i>Paraponera clavata</i>	Guacamayo
QUSF-F 65	<i>Ophiocordyceps</i> sp. 4	COR37B	Hymenoptera	Harpía
QUSF-F 66	<i>Ophiocordyceps</i> sp. 5	COR48	Hymenoptera	Matapalo
QUSF-F 67	<i>Ophiocordyceps</i> sp. 6	COR49	Coleoptera	Matapalo

QUSF-F 68	<i>Cordyceps nidus</i>	COR30	Ctenizidae	Lab TBS
QUSF-F 69	<i>C. nidus</i>	COR82	Ctenizidae	Cabins TBS
QUSF-F 70	<i>Akanthomyces clavata</i>	COR13	Orthoptera	Matapalo
QUSF-F 71	<i>A. clavata</i>	COR54	Orthoptera	Lago
QUSF-F 72	<i>Akanthomyces</i> aff. <i>tuberculatus</i>	COR31	Lepidoptera	Guacamayo
QUSF-F 73	<i>A. tuberculatus</i> aff.	COR53	Lepidoptera	Chichico
QUSF-F 74	<i>A. tuberculatus</i> aff.	COR57	Lepidoptera	Chorongo
QUSF-F 75	<i>A. tuberculatus</i> aff.	COR58	Lepidoptera	Chorongo
QUSF-F 76	<i>A. tuberculatus</i> aff.	COR74	Lepidoptera	Guacamayo
QUSF-F 77	<i>Akanthomyces aculeatus</i>	COR77	Lepidoptera	Chichico
QUSF-F 78	<i>A. aculeatus</i>	COR80	Lepidoptera	Guacamayo
QUSF-F 79	<i>Akanthomyces</i> aff. <i>aculeatus</i>	COR28	Lepidoptera	Lab TBS
QUSF-F 80	<i>Gibellula</i> cf. <i>pulchra</i>	COR75	Opiliones	Guacamayo
QUSF-F 81	<i>Akanthomyces</i> sp. 1	COR21	Ctenideae	Chichico
QUSF-F 82	<i>Cordyceps</i> sp. 1	COR42	Lepidoptera (larva)	Chorongo
QUSF-F 83	<i>Cordyceps</i> sp. 2	COR69	Lepidoptera (larva)	Guacamayo
QUSF-F 84	<i>Torrubiela</i> sp. 1	COR76	Araneae	Lago
QUSF-F 85	<i>Nigelia martiale</i>	COR10	Coleoptera (larva)	Maquisapa

There were a total of 32 identified morphospecies. The Ophiocorycipitaceae family had the most morphospecies (19 spp.), followed by Cordycipitaceae (12 spp.) and lastly the Clavicipitaceae family with only one morphospecies.

The genus with the highest number of collected samples was *Ophiocordyceps* with 64 specimens (75,29%), then *Akanthomyces* with 11 (12,94%), followed by *Cordyceps* s.s. with 4 (4,71%), then *Paraisaria* with 2 individuals (2,71%) and lastly, *Gibellula*, *Hymenostilbe*, *Torrubiela* and *Nigelia* with one specimen (1,18%) each.

Taxonomy

CLAVICIPITACEAE Lindau Earle ex Rogerson, Mycologia 62: 900. (1970), emend. G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora

Stromata are darkly or brightly coloured, fleshy or tough. Perithecia superficial to completely immersed, ordinal or oblique in arrangement. Asci cylindrical with thickened ascus apex. Ascospores usually cylindrical and multiseptate, disarticulating into part-spores or non-disarticulating.

Type: *Claviceps* Tul., Ann. Sci. Nat. Bot., Sér. 3, 20: 43. (1853)

Teleomorphic genera: *Balansia*, *Claviceps*, *Hypocrella*, *Metacordyceps*, *Myriogenospora*, *Neoclaviceps*

Anamorphic genera: *Metarhizium*, *Nomuraea*, *Pochonia*, *Sphacelia* Lév.

Nigelia martiale (Speg.) Luangsa-ard & Thanakitpipattana, comb. nov.

≡ *Cordyceps martialis* Speg. Boletin, Academia nacional de Ciencias, Córdoba 11:535 (1889)

≡ *Metacordyceps martialis* (Speg.) Kepler, G.-H Sung, & Spatafora. Mycologia 104 (1):182–197 (2012)

≡ *Metarhizium martiale* (Speg.) Kepler, Rehner & Humber. Mycologia 106(4):811–829 (2014)

Stromata: Multiple erect, cylindrical to clavate, simple and partly branched, on larvae or pupae of unidentified beetle larva (Coleoptera). Intense orange color, 2,5 cm in length

Perithecia: Same intense orange color, immersed with an oblique arrangement on one face of the stoma.

Notes: *Cordyceps martialis* was first described by Spegazzini (1889) as a new species on a larva of Cerambycidae, (long-horned beetle, Coleoptera) in Brazil. Kepler et al. (2012) sequenced 3 strains of *M. martiale* found on Lepidoptera larvae with bright red or orange stromata. *Nigelia aurantiaca* looks morphologically similar to *N. martiale* but differs in the molecular data, in the type of ascospores and distribution (Luangsa-ard et al., 2017). *N. martiale* ascospores dissociate into part-spores (Mains, 1958). New collections in the Amazon, the type locality of *N. martiale*, should be done to compare these from specimens in Asia since the type specimen is no longer available for study (Luangsa-ard et al., 2017).

OPHIOCORDYCIPTACEAE G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora (2007). MycoBank MB504190.

Stromata vel subiculum fusca vel raro laete colorata, tenacia, fibrosa vel flexibilia, raro carnosae, saepe ostiolis perithecorum prominentibus, summa saepe peritheciis carentia. Perithecia superficialia vel omnino immersa, perpendicularia ad superficiem vel oblique inserta. Asci cylindrici, apice inspissato. Ascospores cylindricae, multiseptatae, maturae in cellulas diffrangentes vel integrae remanentes.

Stromata or subiculum darkly pigmented or rarely brightly coloured, tough, fibrous to pliant, rarely fleshy, often with aperithecial apices or lateral pads. Perithecia superficial to completely immersed, ordinal or oblique in arrangement. Asci usually cylindrical with

thickened ascus apex. Ascospores usually cylindrical, multiseptate, disarticulating into part-spores or nondisarticulating (Sung, Hywel-Jones, Sung, Luangsa-Ard, et al., 2007).

Type: *Ophiocordyceps* Petch, Trans. Brit. Mycol. Soc. 16: 74. (1931)

Teleomorphic genera: *Elaphocordyceps*, *Ophiocordyceps*

Anamorphic genera: *Haptocillium*, *Harposporium Lohde*, *Hirsutella*, *Hymenostilbe*, *paecilomyces-like*, *Paraisaria*, *Syngliocladium*, *Tolypocladium*, *verticillium-like*.

Ophiocordyceps Petch, Trans. Brit. Mycol. Soc. 16: 73. (1931) emend. G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora

= *Cordycepioideus* Stifler, Mycologia 33: 83. 1941.

Stromata or subiculum darkly pigmented or rarely brightly coloured, tough, fibrous, pliant to wiry, rarely fleshy, often with aperithecial apices or lateral pads. Perithecia superficial to completely immersed, ordinal or oblique in arrangement. Asci hyaline, cylindrical, usually with thickened ascus apex, rarely fusoid to ellipsoid. Ascospores usually cylindrical, multiseptate, disarticulating into part-spores or non-disarticulating (Sung, Hywel-Jones, Sung, Luangsa-ard, et al., 2007).

Type: *Cordyceps blattae* Petch, Trans. Brit. Mycol. Soc. 16: 74. 1931.

Anamorphic genera: *Hirsutella*, *Hymenostilbe*, *Paraisaria*, *Syngliocladium*

Ophiocordyceps curculionum (Tul. & C. Tul.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora. MycoBank MB504246.

= *Torrubia curculionum* Tul. & C. Tul., Sel. Fung. Carpol. 3: 20. 1865.

= *Cordyceps curculionum* (Tul. & C. Tul.) Sacc., Michelia 1: 320. 1879.

= *Cordyceps bicephala* subsp. *curculionum* (Tul. & C. Tul.) Moureau, Mém. Inst. Roy. Colon. Belge 7: 50. 1949.



Figure 2. *Ophiocordyceps curculionum* specimens found on Tiputini Biodiversity Station. A, B, D and E) Photo of COR08 and close ups. C) Photo of COR12.

Ophiocordyceps engleriana (Henn.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora.
Mycobank MB504260.

= *Cordyceps engleriana* Henn., Bot. Jahrb. Syst. 23: 538. 1897.

Ophiocordyceps humbertii (C.P. Robin) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora. MycoBank MB504281.

= *Cordyceps humbertii* C.P. Robin, in Tul. & C. Tul., Sel. Fung. Carpol. 3: 18. 1865 (as *C. 'humberti'*).

Ophiocordyceps kniphofioides (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora. MycoBank MB504288.

= *Cordyceps kniphofioides* H.C. Evans & Samson, Trans. Brit. Mycol. Soc. 79: 434. 1982.

Anamorph: *Hirsutella stilbelliformis* H.C. Evans & Samson

Ophiocordyceps lloydii var. *binata* (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora. MycoBank MB504297.

= *Cordyceps lloydii* var. *binata* H.C. Evans & Samson, Trans. Brit. Mycol. Soc. 82: 133. 18: 31. 1984.

Ophiocordyceps nutans (Pat.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora. MycoBank MB504313.

= *Cordyceps nutans* Pat., Bull. Soc. Mycol. France 3: 127. 1887.

= *Cordyceps bicephala* subsp. *nutans* (Pat.) Moureau, Mém. Inst. Roy. Colon. Belge 7: 47. 1949.

Ophiocordyceps unilateralis (Tul. & C. Tul.) Petch, Trans. Brit. Mycol. Soc. 16: 74. 1931.

= *Torrubia unilateralis* Tul. & C. Tul., Sel. Fung. Carpol. 3: 18. 1865.

= *Cordyceps unilateralis* (Tul. & C. Tul.) Sacc., Syll. Fung. 2:570. 1883.

= *Torrubia formicivora* Tul. & C. Tul., Sel. Fung. Carpol. 3: 18. 1865.

= *Cordyceps formicivora* (Tul. & C. Tul.) J. Schröt., Krypt.-Fl. Schlesien 3(2) 27. 1894.

Anamorph: *Hirsutella formicarum* Petch

Ophiocordyceps ponerinarum (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora. MycoBank MB504291.

= *Cordyceps kniphofioides* var. *ponerinarum* H.C. Evans & Samson, Trans. Brit. Mycol. Soc. 79: 441. 1982.

Ophiocordyceps australis Speg. (1883). G.H. Sung, Hywel-Jones, J. M. Sung, Luangsa-ard, Shrestha & Spatafora, Stud. Mycol. 57: 40. (2007)

= *Cordyceps australis* (Speg.) Sacc. In: Syll. fung. (Abellini) 2: 571. (1883)

Paraisaria amazonica (Henn.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora. MycoBank MB504219.

= *Cordyceps amazonica* Henn., Hedwigia 43: 247. 1904

Hymenostilbe Petch, The Naturalist (1931)

Synnemata subcylindric, often slightly attenuated upward, composed of longitudinal more or less parallel closely compacted hyphae (conidiophores). Phialides in a hymenial layer covering the synnema, produced as terminal cells of short lateral branches from the longitudinal hyphae of the synnema or as lateral cells or buds directly from the longitudinal hyphae or less frequently as terminal cells of the longitudinal hyphae, subcylindric to clavate, narrowed above into short sterigmata or obtuse above with short or inconspicuous sterigmata, smooth or variously roughened in the upper portion ; conidia one-celled, hyaline, smooth, single (Mains, 1950).

Type: *Hymenostilbe muscarium* Petch.

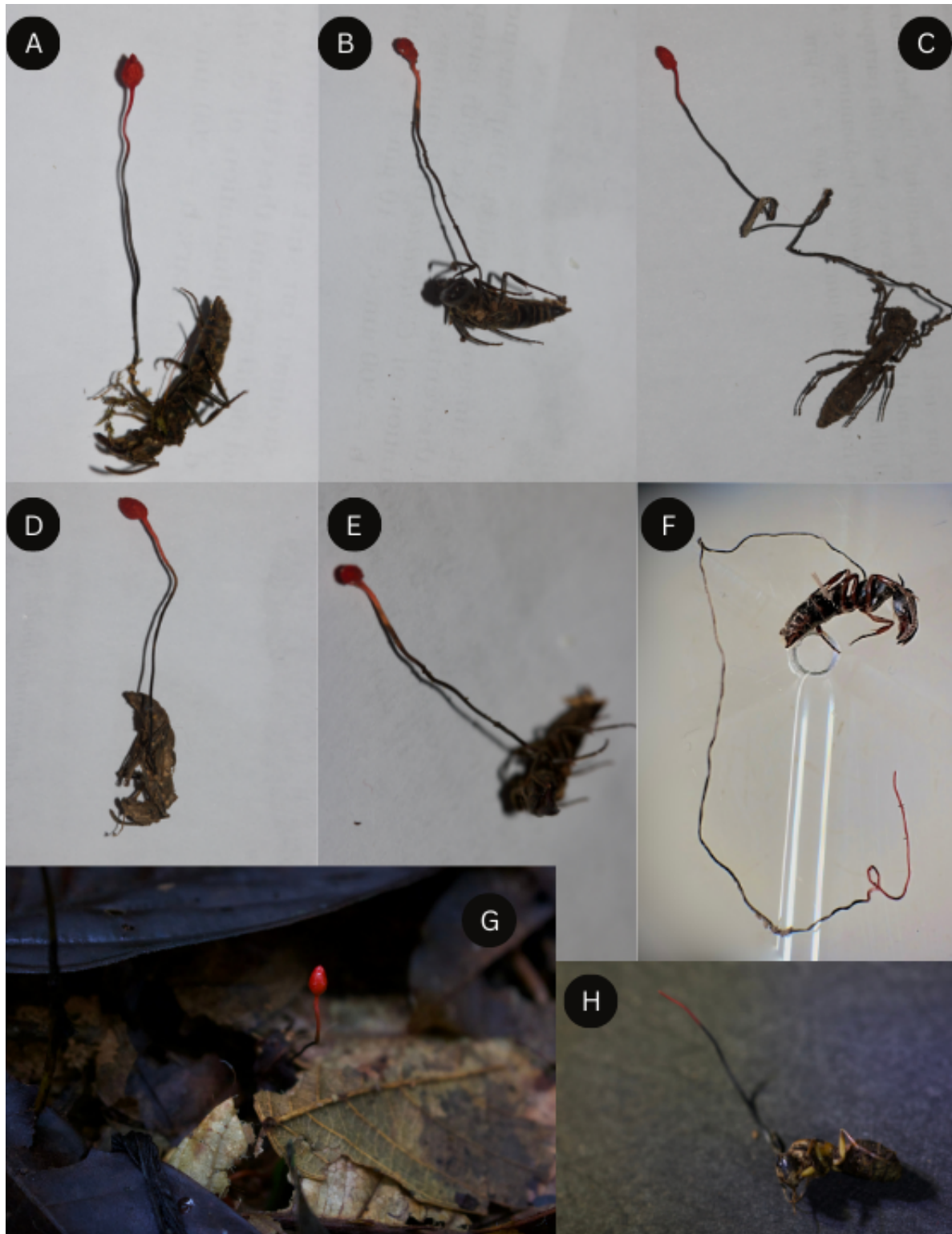


Figure 3. *Ophiocordyceps australis* complex. A-E) Sexual morphs of *O. australis*. F & H) Asexual morphs of *O. australis*. G) Sexual morph on its natural habitat coming out of leaf litter.

CORDYCIPIACEAE Kreisel (1969). ex G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora. MycoBank MB504360.

Stromata vel subiculum pallida vel laete colorata, carnosae. Perithecia superficialia vel omnino immersa, perpendicularia ad superficiem. Asci cylindrici, apice inspissato. Ascospores cylindricae, multiseptatae, maturae diffrangentes vel integrae remanentes.

Stromata or subiculum pallid or brightly pigmented, fleshy. Perithecia superficial to completely immersed, oriented at right angles to the surface of the stroma. Asci cylindrical with thickened ascus apex. Ascospores usually cylindrical, multiseptate, disarticulating into part-spores or remaining intact at maturity (Sung, Hywel-Jones, Sung, Luangsa-Ard, et al., 2007).

Type: *Cordyceps* Fr.

Teleomorphic genera: *Ascopolyporus*, *Cordyceps*, *Hyperdermium*, *Torrubiella*.

Anamorphic genera: *Beauveria*, *Engyodontium*, *Isaria*, *Lecanicillium*, *Microhilum*, *Simplicillium*.

***Cordyceps* s.s.** Fr., *Observ. Mycol.* 2 (revis.): 316. (1818) emend. G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora

= *Phytocordyceps* C.H. Su & H.-H. Wang, *Mycotaxon* 2: 338. 1986.

Stromata or subiculum pallid or brightly pigmented, fleshy. Perithecia superficial to completely immersed, ordinal in arrangement. Asci hyaline, cylindrical with thickened ascus apex. Ascospores hyaline, cylindrical, multiseptate, disarticulating into part-spores or nondisarticulating, rarely possessing a thread-like structure connecting the fusiform ends (Sung, Hywel-Jones, Sung, Luangsa-Ard, et al., 2007).

Type: *Cordyceps militaris* (L.: Fr.) Fr., *Observ. Mycol.* 2 (revis.): 317. (1818)

Anamorphic genera: *Beauveria*, *Isaria*, *Lecanicillium*, *mariannaea*-like, *Microhilum*, *Simplicillium*.

Notes: Samples COR42 and COR 69 were identified inside this genus because of morphological similarities to the description made by Sung et al. (2007).

Gibellula pulchra Cavara, *Atti Ist. bot. R. Univ. Pavia*, 2 sér. 3: 347 (1894).

= *Torrubiella arachnophila* var. *pulchra* Mains, *Mycologia* 42: 316 (1950).

= *Torrubiella pulchra* (Mains) Koval, *Klavitsipital'nye Griby SSSR*: 71 (1984).

Notes: The genus *Gibellula* is known to be a pathogen for spiders that produce primarily synnematus, aspergillus-like conidiophores with terminal vesicles, which give rise to phialides produced on metulae. Molecular phylogenies by Sung et al. (2007) placed *Gibellula* species in a single clade along with *torrubiella*-like sexual morphs. Sample COR75 matches with morphological and host description.

Torrubiella Boud., in Rev. Myc. 7: 227 (1885).

Stromata pulvinata vel plana, haud stipitata, varie colorata. Hypothallus hyalinus. Perithecia in stromate vel in hypothallo formata, elongate lageniformia vel conica, luteo-brunnea vel purpureo-rubida. Asci cylindrici, in summo inspissati. Ascospores filiformes, multiseptatae, in cellulas dilabentes an non.

Stromata pulvinate to planar, not stipitate, variously coloured. Hypothallus hyaline. Perithecia produced on the stroma or hypothallus, elongated flask-shaped to conical, yellow–brown to purple–red. Asci cylindrical with thickened ascus apex. Ascospores filiform, multiseptate, disarticulating or non-disarticulating into part-spores (Kobayasi, 1982).

Type: *Torrubiella aranicida* Boud.

Stromata: Growing mainly on Arachnidae and Coccidae, rarely on other insects. Mycelial mat formed on host bodies.

Perithecia: Superficial, gregarious on mycelial mat. Secondary ascospores fusiform or truncated cylindrical.

Notes: *Torrubiella* has been shown to be polyphyletic, including astipitate taxa throughout Cordycipitaceae and Hypocreales (Kepler et al., 2017). The status of *Torrubiella* is complicated because of the uncertain phylogenetic placement of the type species, *T. aranicida*. The type species of *Torrubiella*, *T. aranicida*, known from a spider in France. Its original description indicated an asexual morphology that more closely approximates *Lecanicillium* or *Simplicillium*. However, several morphological characteristics of *T. aranicida* are very similar to those of the *Akanthomyces* genus. These include the superficial and separated arrangement of the perithecia and the lack of a subiculum in the type specimen as shown in Johnson et al. (2009). Some sexual morphs currently under the *Akanthomyces* genus have *torrubielloid* ascomata, specifically *A. coccidioperitheciatus* on spiders, *A. lecanii* on scale insects, and *A. tuberculata* on moths (Kepler et al., 2017).

Akanthomyces Lebert, Z. Wiss. Zool. 9: 449 (1858).

Synnemata cylindrical often somewhat attenuated upward, composed of longitudinal, more or less parallel, closely compacted hyphae (conidiophores). Phialides in a hymenial layer

covering the synnema or in *A. areanearum* somewhat scattered over the surface, produced as terminal cells of short lateral branches from the outer hyphae or arising as lateral cells or buds of the outer hyphae of the synnema, or less frequently terminating the hyphae of the synnema, ellipsoid, obovoid or cylindric usually more or less acute at the apex and terminating in a short sterigma, smooth or roughened ; conidia one-celled, hyaline, smooth, catenulate (Mains, 1950).

Type: *Akanthomyces aculeatus* Lebert, Z. Wiss. Zool. 9: 449 (1858).

Notes: The genus *Akanthomyces* primarily infects Lepidoptera, but also spiders and locusts (Orthoptera). It forms a clade distinct from *Beauveria* and *Cordyceps* (Aini et al., 2020). It includes the moth pathogen *Cordyceps tuberculata*, which is linked to an asexual morph described as *A. pistillariiformis* (Samson & Evans, 1974). Other fungi in this clade include *C. coccidioperitheciata* (on spiders) and *C. confragosa* (on scale insects) both with torrubielloid perithecia. The morphological characters associated with *Akanthomyces* are also found in a clade of spider-pathogenic species sister to the *Gibellula* clade (Kepler et al., 2017).

Akanthomyces tuberculatus Lebert. (1858). Spatafora, Kepler & B. Shrestha. (2017)
MycoBank MB820863

= *Cordyceps tuberculata* (Lebert) Maire, Bull. Soc. Hist. Nat. Afrique N. 8: 165 (1917).

= *Isaria pistillariiformis* Pat., Bull. Soc. Mycol. Fr. 9: 163 (1893); as “*pistillariaeformis*”.

= *Insecticola pistillariiformis* (Pat.) Mains, Mycologia 42: 579 (1950); as “*pistillariaeformis*”.

= *Akanthomyces pistillariiformis* (Pat.) Samson & H.C. Evans, Acta Bot. Neerl. 23: 29 (1974).

Basionym: *Akrophyton tuberculatum* Lebert, Z. Wiss. Zool. 9: 448 (1858).

Akanthomyces aculeatus Leb. Zeitsch. wissen. Zoologie 9 : 447. (1858).

Yellowish mycelium more or less covering adult moths and attaching them to the substratum. Synnemata arising from various parts of the insect, often developing from conical masses of mycelium, narrowing upward, very variable in length, 1-8 mm. long, slender, 0.1-0.5 mm. thick, yellowish, composed of longitudinal somewhat interwoven hyphae. Phialides densely compacted into a layer covering the synnema, terminating the hyphae or arising directly as lateral cells from the outer hyphae of the synnema or terminating short lateral branches, subcylindric or narrowly ellipsoid, 6-16 x 2.5-4 µm narrowing above to an acute apex terminated by a short sterigma up to 4 µm long, smooth. Conidia broadly ellipsoid or obovoid often acute at the lower end, 3-6 x 2-3 µm, smooth, hyaline catenulate (Mains, 1950).

Notes: Even if it is described as a type species, *A. aculeatus* has been lately rearranged as the anamorph of *A. tuberculatus* (YongDong et al., 2016). Therefore, the 3 specimens of *A. aculeatus* found in Tiputini could be the asexual stages of the *A. tuberculatus* species.

Akanthomyces clavata Mains. Mycologia 42: 566-589, (1950), K.T.Hodge. Evo. Bio. Chem. Biocon. & Cul. Imp. (2003).

= *Insecticola clavata* Mains. Mycologia 42: 566-589, (1950)

Synnemata multa, pallide brunnea, clavata, 0.5-2.0 mm. longa; stipites 60-250 μm crassi, ex longitudinalibus hyphis compositi; superae fertiles partes subcylindricae, obovoideae vel ellipsoideae, interdum furcatae, 300-1500 μm longae, 102-500 μm . crassae, hymeniis phialidium tectae; phialides subcylindricae, 17.1-21.4 x 2.8-4.3 μm P., superne acutae, brevis sterigmatibus; conidia ellipsoidea vel oblonga, 4.5-8.5 x 2.1-2.5 μm P., hyalina, catenulata.

Mycelium thin brown partly covering insect; synnemata numerous, arising from various parts of the host, light brown, clavate, 0.5-2.0 mm. long; stipes 60--250 μm thick, composed of longitudinal parallel compact hyphae 2-4 μm wide, the outer brownish ; the fertile portions of the synnemata terminal, subcylindric, obovoid or ellipsoid, occasionally furcate, 300-1500 μm long, 102-500 μm thick, covered with a compact hymenium of phialides, often white and pulverulent from adhering masses of conidia; phialides subcylindric, 17.1-21.4 x 2.8-4.3 μm narrowing above to acute apices, terminated by short sterigmata; conidia ellipsoid to oblong, 4.5-8.5 x 2.1- 2.5 μm , hyaline, catenulate (Mains, 1950).

Notes: The small synnemata are scattered on various parts of the insect, specially upon the legs, antennae and between the segments of the body. The longitudinal parallel hyphae of the stipes diverge outward repeatedly branching to form the upper compact fertile parts of the synnemata. The phialides are located at the end of the branches to form a compact hymenium.

Cordyceps nidus T. Sanjuan, J.S. Chiriví-Salomón & S. Restrepo, (2017). PLoS One. 12(6): e0179428. Mycobank MB817601

Etymology: In reference to the burrow of the trapdoor spiders.

Stromata claviform, simple, gregarious, fleshy, 10-42 mm long. Fertile part subcylindrical, apex rounded, pruinosa, coral-red (8B6) to carmine red (9A8) 2.5-18 x 0.5-3 mm. Stipe terete, smooth, brownish red (9C7), 5-34 x 0.5-2 mm. Perithecia pseudoimmersed, perpendicular orientation, ellipsoid, 300-500 (-630) x 110-190 (-205) μm (n = 40). Asci cylindrical, (145-) 190-360 x 2-4 μm (n = 50), cap 3-4.2 x 1.2-3 μm . Ascospores filiform, hyaline, 100-120 x 1.0 μm (n = 5); breaking irregularly into truncate partspores, (4-) 6-10 x 1 μm (n = 50) (Chiriví et al., 2017).

Note: The etymology of *C. nidus* is based on the host it infects, that is the trapdoor spiders of the Idiopidae family. It has been reported only in the tropical rainforests of Ecuador and Colombia (Chiriví et al., 2017). White mycelia cover the spider and the burrow like a net connected to the stromata coming out of the lid.



Figure 4. Some of the collected *Cordyceps* s.l. included in this study. A) *O. engleriana* from above. B) Sideview of *O. engleriana*. C) *A. clavata* in situ. D) *Acanthomyces* sp. on a Ctenideae spider. E) Magnified image of *O. unilateralis*. F) *C. nidus* partly removed from the floor to make visible the trapdoor spider covered in white mycelium. G) *O. lloydi* var. *binate* on the underside of a palm leaf. H) *A. tuberculatus* on a moth. I) *N. martiale* on unidentified larva. J) Another variation of *C. nidus*. K) Two ants infected by *O. unilateralis* on a particular position. L) *P. amazonica* in situ coming out of leaf litter.

Morphospecies and amount of collected samples to each are specified of Table 2. Some are shown on Figure 4. Number of samples per genera are listed on Attachment 1.

Table 2. Identified morphospecies and abundance

Family	Morphospecies	n
Ophiocordycipitaceae	<i>Hymenostilbe sp.</i>	1
	<i>Ophiocordyceps australis</i>	11
	<i>Ophiocordyceps nutans</i>	3
	<i>Ophiocordyceps curculionum</i>	4
	<i>Ophiocordyceps cf. curculionum</i>	1
	<i>Ophiocordyceps engleriana</i>	1
	<i>Ophiocordyceps kniphofioides</i>	1
	<i>Ophiocordyceps aff. kniphofioides</i>	2
	<i>Ophiocordyceps aff. ponerianum</i>	2
	<i>Ophiocordyceps aff. unilateralis</i>	29
	<i>Paraisaria amazonica</i>	2
	<i>Ophiocordyceps aff. humberitii</i>	1
	<i>Ophiocordyceps lloydi var. Binata</i>	3
	<i>Ophiocordyceps sp. 1</i>	1
	<i>Ophiocordyceps sp. 2</i>	1
	<i>Ophiocordyceps sp. 3</i>	1
	<i>Ophiocordyceps sp. 4</i>	1
	<i>Ophiocordyceps sp. 5</i>	1
	<i>Ophiocordyceps sp. 6</i>	1
	Cordycipitaceae	<i>Cordyceps nidus</i>
<i>Akanthomyces clavata</i>		2
<i>Akanthomyces aff. tuberculatus</i>		5
<i>Akanthomyces aculeatus</i>		2
<i>Akanthomyces aff. aculeatus</i>		1
<i>Gibellula cf. pulchra</i>		1
<i>Akanthomyces sp. 1</i>		1
<i>Cordyceps sp. 1</i>		1
<i>Cordyceps sp. 2</i>		1
<i>Torrubiela sp. 1</i>		1
Clavicipitaceae	<i>Nigelia martiale</i>	1

The host composition comprises 8 orders. A total of 54 of the collected samples were parasitizing on Hymenoptera hosts (63,53%), 53 on ants (Formicidae) and one on a wasp

(Vespidae, Suborder Apocrita). The second most common host group is the Lepidoptera order (11,76%) with 8 adult moths and other 2 as caterpillars. Mosts of the lepidopteran hosts were identified to the Noctuidae family and one host into Sphingidae (COR57). The following host group belongs to the Coleoptera order (8,24%) with 4 host individuals identified into the Curculionidae family, one was identified to the *Pselaphacus nigropunctatus* species. Only one host in a larval stage. The next host group is the Araneae order with 5 individuals (5,88%) of which 2 were identified into the Ctenizidae and one into the Ctenideae family. The Orthoptera order occupies the next place with 4 parasitized individuals (4,71%). The Hemiptera host group has 3 individuals (3,53%) all of which were identified into the Pentatomidae family. The last 2 host groups with 1 specimen (1,18%) are the Diptera order and Opiliones.

Among the 7 different host orders a variety of entomopathogenic fungi morphospecies were found. In the Araneae host group it was found a total of 5 morphospecies, in the Coleoptera group 3 morphospecies, one for Diptera, one for Hemiptera, 12 species for Hymenoptera, 5 for Lepidoptera, 2 species for Orthoptera and 1 for Opiliones.

The most common *Cordyceps* s.l. were species of the *O. unilateralis* complex with 29 specimens parasitizing ants of the *Camponotus* genus. The next most common species are the 11 samples of the *O. australis* complex parasitizing ants of the Ponerinae family. Three samples of *O. kniphofioides* from which 2 parasitized Ponerinae ants and one the infamous conga ant (*Paraponera clavata*). The morphospecies *Ophiocordyceps* sp. 1 (COR14A) and 2 (COR14C) were found growing alongside one specimen of *O. ponerianum* aff. (COR14B) on the same ant. Two additional samples parasitizing conga ants were *O. ponerianum* aff. and *Ophiocordyceps* sp. 4. Only one sample of *O. humbertii* was found growing on a wasp.

Nearly all of the Lepidoptera order included specimens parasitized by the *Akanthomyces* genus. The 5 samples of *A. tuberculatus* complex alongside the 3 samples of *A. aculeatus* were found parasitizing moths. The sample COR42 of *Cordyceps* sp. 1 parasitized on an unidentified spiky caterpillar. The sample COR69 of *Cordyceps* sp. 2 grew on a very small (6 x 0,5 mm) caterpillar found on a leaf at 1,70 m from the forest floor.

In the Coleoptera order there are 4 samples of *O. curculionum* found growing on true weevils (Curculionidae). COR04 was found on another unidentified beetle. The sample of *Nigelia martiale* (COR10) was found on an unidentified beetle larva. The sample of *Ophiocordyceps* sp. 6 was parasitized by another fungi of the genus *Niveomyces* sp. found on a very digested beetle.

In the Araneae order 2 specimens of *C. nidus* were found parasitizing trapdoor spiders (Ctenizidae), one sample of *O. engleriana* on the underside of a leaf at a height of 1,5 m, one specimen of *Gibellula* cf. *pulchra*, and one *Akanthomyces* sp. infecting a Ctenideae spider found on top of leaf litter.

The Orthoptera order comprised of 2 grasshoppers parasitized by *P. amazonica* found under leaf litter, and another 2 infected by *A. clavata*. Both found stuck to plant branches at no more than a meter high.

The 3 samples of *O. nutans* were found on stink bugs (Pentatomidae). All of them found under leaf litter on the side of the trails. And lastly, the only Diptera host was parasitized by *Hymenostilbe sp.* found on top of a leaf at 1,5 meters high.

The distribution of habitat of the collected samples is relatively uneven. A total of 69 samples with 22 species were found on Terra Firme Forest. While only 16 samples with 9 species were found on Varzea forest habitat. All samples were found on 13 locations including all main trails and structures of TBS and ECY river port. The most sample-abundant trail is Guacamayo with 22 collected samples (25,88%), followed by Matapalo with 16 samples (18,82%), then Chichico with 11 samples (12,94%), Harpía with 9 samples (10,59%), Chorongó with 8 (9,41%), Lab TBS, Lago and TBS dining hall with 4 specimens (4,71%) each, Maquisapa and Numa with 2 samples (2,35%) each, Cabins TBS, ECY harbor and Mata-Mata with 1 sample (1,18%) each.

Even if the difference in diversity between the 2 habitats might seem obvious, no statistical test found significant differences. A comparison between the two habitats was established with the Shannon Diversity Index (SDI) which took into consideration the number of species, their abundance and location. For the Terra Firme habitat an SDI of 2,58 was obtained with an evenness of 0,836 and an average population of 3,14 per morphospecies. While the Varzea habitat resulted in a SDI of 1,89 with an evenness of 0,862 and an average population of 1,78 per morphospecies.

CONCLUSIONS

This study presents new insights into the diversity of *Cordyceps* s.l. fungi in the Ecuadorian northern Amazon, specifically inside Tiputini Biodiversity Station. The amount of time spent in the location limited the quantity of collected samples and the profundity of this research. Nonetheless, the collected information serves as a foundation on diversity studies that take the fungi kingdom into consideration.

It is of extreme importance to conduct further research on these fungi since most diversity studies neglect fungi in their statistics. But most of all because of the meaning this megadiverse area means to the world and the importance these organisms have on population dynamics. The Yasuní National Park is threatened by the most aggressive oil and mining industry. Not so far of TBS lies one of the biggest oil extraction facilities in Ecuador. Even from a couple hundred meters away the constant flame is visible at night from inside TBS, a safe zone for flora, fauna and funga.

Studying these organisms reveal a new dimension of the population dynamics happening in the Amazon rainforest. Not only specimens belonging to all the 3 families that make up the entomopathogenic fungi group were found in this study, but also an abundant and diverse samples were found and collected. This gives us already a simple overview of the vast diversity these fungi have inside TBS. It is still needed to study these organisms during the so called dry season to better understand the diversity fluctuation throughout the year. That way it is easier to better record the existing *Cordyceps* s.l. diversity and approximate the total number of species present in TBS.

The information that was included in the data collection also shows how these parasitic fungi may influence the population of insects and spiders in these ecosystems. This study initially started as a comparative study of the two habitats found in TBS, Varzea and Terra-Firme. But during the time this study was conducted it was also rainy season. That means that the floody terrain (varzea) is mostly underwater and is difficult to mobilize and search for fungi when water is nearly 2 m. deep.

Although the endemic species *O. tiputini* was not found, there were other native species that are emblematic to the Amazonian rainforest, such as *O. unilateralis* or *P. amazonica*. The morphological identification was limiting without the proper microscopic work. Given that limitation, it was opted to focus on tissue sampling for molecular work that would contribute

to identification to the species level and, if there is the case, to discover new species that were not reported to science before. Even so, it helps to differentiate species within the same complex that morphologically look very similar and are hard to tell apart. Molecular tools also help to tell apart sexual from asexual stages from the same species and so comply with the “One fungus, one name” norm when identifying *Cordyceps* s.l.

Since considerable changes to the taxonomy of *Cordyceps* s.l. have occurred since research on entomopathogenic fungi entered the molecular era, it is strictly necessary to genetically identify these organisms through DNA barcoding. This is mainly a descriptive study and as such, it aims to settle a foundation for new research projects with these fungi to flourish in Ecuadorian Academia.

DISCUSSION

Although most described species reside along the tropics, known species richness of this particular group varies considerably between geographic regions and it seems to be correlated with the amount of research effort (Palfner et al., 2012). Historically, most reported species come from Asia, especially Japan and China (Kobayasi, 1982; Sung, Hywel-Jones, Sung, Luangsa-Ard, et al., 2007). However, nowadays more research has been done in the amazon rainforest and other tropical and subtropical regions (Aini et al., 2020; Araújo et al., 2020; Chiriví et al., 2017), leading to the discovery of new species and recategorization of existing taxons with help of molecular tools.

In the past decade more than 20 different species that belong to the *O. unilateralis* and *O. australis* complexes have been described in Brazil thanks to the work of Araujo and Evans (Araújo et al., 2015, 2018, 2020; Evans et al., 2011). A *Cordyceps* diversity assessment in Argentina revealed a total of 22 species recorded for the whole country, based mostly on herbarium specimens and some collected samples (Catania et al., 2018). Whereas in Japan a recent *Cordyceps* and allies reassessment described a total of 31 species (Sato et al., 2022). Species composition in Tiputini varies very little with neighboring countries and even continental Asia. However, species composition changes almost completely when compared to Japan. This gives a little perspective on the amount of *Cordyceps* diversity found in this study, 32 mophospecies, in just ten days and within just one location.

Even if entomopathogenic fungi are expected to increase in richness in the tropics, the relatively low record of these fungi in South America may be due to the limited distribution of many species, which in some cases can be restricted to a single location (Palfner et al., 2012). This makes this biodiversity study all the most important to asses the local diversity and include them in diversity indexes, where most funga is neglected. On the other hand, some hosts have complex and extensive life cycles, which leave only a narrow window in time for the fungi to infect their respective host and so study them whilst this process is visible. Due to logistical and safety reasons the canopy area was not included and studied. Although it is expected that a different species composition is found higher up the forest.

Based on the descriptions of *O. australis* (Evans & Samson, 1982) and *O. curculionum* (Mains, 1947), both have very similar morphological structures. Their differentiation was made based on their hosts. The species *O. australis* (samples COR15, COR16, COR17, COR18, COR26, COR81 and COR59) parasitizes mainly ants of the Ponerinae family (Figure 3). Specimens COR02, COR07, COR22 and COR51 don't have the typical capitated peritecia but presented the red coloration at the end of the black stromata, typical of the asexual morph of the *O. australis* complex. On the other hand, *O. curculionum* specimens (COR04, COR06, COR08, COR12 and COR38) infect true weevils, members of the

Curculionidae family (Figure 2). A very similar identification difficulty was encountered with sample COR38, which lacks the capitated form of the perithecium, but still presented the coloration difference from black stroma to red ending. Only genetic sequencing from extracted tissue of those samples will identify them correctly.

A similar difference between samples identified to the same species, but with coloration difference is presented with the *O. nutans* samples COR03 and COR39. The colorations of COR03 are as described for *O. nutans* type (Sanjuan et al., 2015). Interestingly, the morphological structure of COR39 is identical as COR03, varying only in coloration of the peritecia. COR39 has brown coloration, while peritecia of COR03 is bright orange. This might be related to the age of the specimen, COR39 being a more mature and probably a decaying specimen.

The most abundant *Ophiocordyceps* found in this study were species inside the *O. unilateralis* complex. Although their specific identification may seem impossible without genetic sequencing due to their small size, most share either identical coloration, structure, location of perithecium and size (Araújo et al., 2015). To narrow the possible species in this complex a correct identification of the hosts should be made to compare with Araújo and Evans findings of the Amazonian zombie-ant fungi (Araújo et al., 2018; Evans et al., 2011)

Samples COR14C, COR48 and COR49 remained as morphospecies *Ophiocordyceps sp.* due an interesting find that hinders the *Cordyceps* identification. These samples were found parasitized by the newly described hyperparasite *Niveomyces sp.* (Araújo et al., 2022). Which until now has only been reported in Florida, Africa, Australia and Brazil. Other interesting scenario is the fact that COR14A, COR14B and COR37A and CORB were found with different morphospecies growing on the same host. It can also be considered an anamorph of the identified COR14B *O. ponerianum* or this case might be a rare example of multiple species parasitizing and fruiting on the same host at the same time.

The only *Ophiocordyceps* found infecting a wasp was identified as *O. humberitii* due to stroma distribution along the host (Somavilla et al., 2020). The description of mature specimens of *O. humberitii* describe much larger fructification of the fungi, but it might just be that the found specimen was still on growing process. Most observations of *O. humberitii* in Ecuador are found in the Galapagos islands, although all of them are asexual morphs. Here in Tiputini, sample COR41 is clearly a sexual morph (teleomorph) and it was even found at eye level.

One of the rarest samples is COR75 with a *Gibellula cf. pulchra* parasitizing an Opiliones host. Opiliones differentiate themselves from their arachnid cousins the spiders by possessing bilateral exocrine glands on the dorsal side of their cephalotorax that produce defensive secretions that protect them against external pathogens and parasites (Cokendolpher, 1993). For that reason, not many cases of Opiliones infected by *Cordyceps s.l.* have been registered.

They are not immune to them nonetheless. Under stereoscopic observation, the host of COR75 is most likely a member of Opiliones, nevertheless, there is also a chance that the host is a spider so digested that the head section fell off and the abdomen of the spider gets confused as a cephalotorax of the Opiliones.

The ecology of these fungi still needs further research. There is still a lot of field work needed to better understand their role in population dynamics. These samples are still to be better described once the molecular work is finished. Until then, this study aims to describe an uncomprehended fungi group. The description of the species composition serves as a baseline for fungal diversity and conservation studies that hopefully will help to protect this unique area.

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ATTACHMENT A:

Attachment 1. Number of collected samples per genus

