What's in Your Head, Zombie? *Camponotus renggeri* Ants Parasitized by the Entomopathogenic Fungus *Ophiocordyceps camponoti-renggeri* in a Relic of Atlantic Forest in Caatinga Biome, Brazil

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ABSTRACT – Entomopathogenic fungi are widely known to parasitize and manipulate the behavior of various orders of arthropods. In this study, we recorded parasitism involving the entomopathogenic fungus *Ophiocordyceps camponoti-renggeri* and host ants of the species *Camponotus renggeri* in a relic of Atlantic Forest in Caatinga biome, in addition to characterizing the environmental and ecological aspects of the interaction. We found 210 infected ant workers, fixed predominantly on the margins of the abaxial face of leaves of the local vegetation. Most ants used simple phyllotaxis leaves for fixation and death, whose size varied widely. The parasitized ants died about 1.5 m above the ground. These results suggest that *Ophiocordyceps camponoti-renggeri* has high virulence and that the behavioral changes induced in its hosts favor their fitness.

Keywords: Biodiversity; formicidae; negative interaction; parasitism; pathogen.

O que Tem em Sua Cabeça, Zumbi? Formigas *Camponotus renggeri* Parasitadas pelo Fungo Entomopatogênico *Ophiocordyceps camponoti-renggeri* em um Relicto de Mata Atlântica no bioma Caatinga, Brasil

RESUMO – Fungos entomopatogênicos são amplamente conhecidos por parasitar e manipular o comportamento de várias ordens de artrópodes. Neste estudo, registramos o parasitismo envolvendo o fungo entomopatogênico *Ophiocordyceps camponoti-renggeri* e formigas hospedeiras da espécie *Camponotus renggeri* em um relicto de Mata Atlântica no bioma Caatinga, além de caracterizar os aspectos ambientais e ecológicos da interação. Encontramos 210 formigas operárias infectadas, fixadas predominantemente nas margens da face abaxial das folhas da vegetação local. A maioria das formigas usava folhas de filotaxia simples para fixação e morte, cujo tamanho variava amplamente. As formigas parasitadas morreram cerca de 1,5 m acima do solo. Esses resultados sugerem que *Ophiocordyceps camponoti-renggeri* possui alta virulência e que as mudanças comportamentais induzidas em seus hospedeiros favorecem sua aptidão.

Palavras-chave: Biodiversidade; formicidae; interação negativa; parasitismo; patógeno.

¿Qué Hay en Tu Cabeza, Zombi? Hormigas *Camponotus renggeri* Parasitadas por el Fongo Entomopatógeno *Ophiocordyceps camponoti-renggeri* en un Relicto de Floresta Atlántica en el bioma Caatinga, Brasil

RESUMEN – Los hongos entomopatógenos son ampliamente conocidos por parasitar y manipular el comportamiento de varios órdenes de artrópodos. En este estudio registramos el parasitismo que involucra al hongo entomopatógeno *Ophiocordyceps camponoti-renggeri* y hormigas hospederas

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de la especie *Camponotus renggeri* en un relicto de Mata Atlántica en el bioma Caatinga, además de caracterizar los aspectos ambientales y ecológicos de la interacción. Encontramos 210 hormigas obreras infectadas, fijadas predominantemente en los márgenes de la cara abaxial de las hojas de la vegetación local. La mayoría de las hormigas usaban hojas de filotaxia simples para adherirse y matar, cuyo tamaño variaba ampliamente. Las hormigas parasitadas morían aproximadamente a 1,5 m del suelo. Estos resultados sugieren que *Ophiocordyceps camponoti-renggeri* tiene una alta virulencia y que los cambios de comportamiento inducidos en sus hospedadores favorecen su fitness.

Palabras clave: Biodiversidad; formicidae; interacción negativa; parasitismo; patógeno.

Introduction

Fungi represent the second largest group of eukaryotic organisms with 120,000 species currently accepted (Hawksworth & Lücking, 2017), representing 6.6% of the total estimated species in the world (Hawksworth, 2001). Because they are heterotrophic, fungi need to absorb organic compounds as a source of energy for their growth (Cooke & Swhipps, 1980). By reason of this biological characteristic, fungi evolve as saprophytes, feeding on dead organic matter, or symbionts, maintaining close associations with other living organisms (Maccheroni et al., 2004). In addition, they can act as parasites, being closely linked to the host, penetrating or degrading tissues to absorb essential substances for their development, causing the host's death or disability (Delgado & Murcia, 2011; Araújo & Hughes, 2016). When they have this biological character, they are classified as entomopathogenic fungi (Mora et al., 2017).

About 700 species and 90 genera of entomopathogenic fungi have been described (Khachatourians & Qazi, 2008). These organisms are known to form parasitic relationships with different orders of arthropods (Shrestha et al., 2016; Sobczak et al., 2020), causing about 80% of the diseases that affect insects (Alves, 1998). In general, these interactions occur in the form of epizootics, causing the contamination of a significant number of ant individuals in tropical forests (Andersen et al., 2009). After infection of the hosts, *Ophiocordyceps* sp. it commonly advances in its development through several stages until reaching maturity and effectively dispersing (Andersen et al., 2012). In some cases, the parasites adaptively manipulate the behavior of the hosts to increase their "fitness", taking the host to places favorable to the efficient dispersion of their spores, thus increasing the transmission to new hosts (Araújo & Hughes, 2016).

The behavioral manipulation of hosts is considered a phenotypic extension of the parasitic organism (Dawkins, 1982), given that the atypical behavior developed in the host is not caused by the expression of its own genes, but by the genes belonging to the parasite (Hughes & Libersat, 2019). Thus, the parasite uses the host only as a vehicle for the dispersion and transmission of its genes, increasing its adaptive value (Dawkins, 1982; Hughes, 2013). According to Hughes et al. (2011), the behavioral alteration of "zombie" ants is triggered by the infection in the animal's brain, which induces the host to seek mainly the leaves of the plants to fix their jaws and, later, to die ("death grip").

The zombification induced by fungi of the *Ophiocordyceps unilateralis* complex (Ophiocordycipitaceae: Hypocreales) in ants of the *Camponotus* genera (Formicinae: Formicidae) is well documented in several tropical forests around the world (Loreto et al., 2014; Araújo et al., 2015, 2018), highlighting the wide geographical distribution of this interaction. Given the climatic and environmental conditions, tropical forests are the most favorable region for the occurrence of parasitism in ants caused by entomopathogenic fungi (Evans, 1974; Araújo et al., 2018). In the Brazilian Amazon, for example, natural epizootics have been recorded in adult individuals of *Camponotus* sp. caused by fungi *O. unilateralis* complex (Andrade, 1980; Andriolli et al., 2019). In the state of Ceará, remnants of the Atlantic Forest are areas with high potential for carrying out studies that demonstrate the importance and ecological and evolutionary significance of parasitic interactions between different groups of organisms (Sobczak et al., 2017a, 2017b, 2020).

Although many recent discoveries have been published, little is known about the distribution of species of entomopathogenic fungi and the ecology of their associations with arthropod hosts, mainly with ants. This fact is more aggravating considering that *Camponotus* spp. is one of the most species-rich genus with 1,524 species currently described with pandemic distribution (Janicki et al., 2016; Antweb, 2020; Antmaps, 2020), with diverse and well distributed workers by forest strata and dominant species that can change the regional diversity and ecosystem dynamic (Vicente & Izzo, 2021; Silva-Viana et al., 2021; Vicente et al., 2016). Among the *Camponotus* species, *Camponotus renggeri* Emery, 1894 has the known distribution from Panamá to Uruguay (Brandão, 1991; Basset et al., 2012). Thus, the aim of this study was to know and characterize the ecological and environmental aspects of parasitism involving the entomopathogenic fungus *Ophiocordyceps camponoti-renggeri* Araujo et al., 2015 and the host ant *Camponotus renggeri* Emery, 1894, as well as expanding the area of occurrence of this interaction.

Material and Methods

Study area

The study was conducted on the Purgatório trail (4° 13.355 'S, 38° 53.732' W), located in the humid forest of the municipality of Pacoti, Ceará state, Brazil. With 400 m of extension, the trail is inserted in the area of Maciço de Baturité, a Conservation Unit of the state of Ceará that covers 32,690 hectares distributed in 13 municipalities of the region (Nascimento et al., 2010). The Serra de Baturité (4° 4 '30 "S and 38° 52' 39.15 W) represents the main geographic reference of the Maciço de Baturité, being characterized as a type of humid enclave within the semiarid region, with average annual temperature and precipitation of 20.8° C and 1,221 mm, respectively (PDITS, 2008).

Due to its geographical location and altitude varying from 600-1100 m, the Serra da Baturité contains in its highest areas a complex and diversified vegetation that acts as an ecological refuge for many species of animals, in addition to offering essential conditions for the supply of different hydrographic basins in the region (PDITS, 2008). These humid forests contain remnants of the forest complex of the Atlantic Forest and the Amazon Forest. Because of this, they have great biodiversity and high rates of endemism (Rebouças et al., 2021; Moro et al., 2015).

Data sampling

Two exploratory field expeditions were carried out in February 2019 and January 2020, both during rainy season, in order to register and collect specimens of *Camponotus* ants parasitized by entomopathogenic fungus. In the first expedition, a visual search for infected ants was carried out along the trail. All ants that had a death grip on the vegetation were collected and placed in sterile microtubes using tweezers. The samples were taken to the Laboratory of Ecology and Evolution of University of International Integration of Afro-Brazilian Lusophony (UNILAB), where photos of the specimens and the division of the stage of development in which the fungi were found were taken. At this time, the stage of development of the parasitic fungus was categorized into four phases: Fresh, Stroma, Mature and Hyperparasitized (Andersen et al., 2012). Subsequently, the samples were sent for taxonomic identification at the Laboratório de Mirmecologia – Centro de Pesquisas do Cacau (CEPEC-CEPLAC), Bahia state, Brazil, to the taxonomist Jacques Hubert Charles Delabie.

Results

We recorded a total of 210 *Camponotus renggeri* worker ants parasitized by the fungus *Ophiocordyceps camponoti-renggeri* on leaves of 177 plants (Fig. 1A) during the two expeditions. All infected ants contained an external mycelium that covered parts of the mesosome and mandible, in addition to stroma with a mature fruiting body projected outside the host's body (Fig. 1B). In the first expedition, 137 ants infected with the fungus were found. As for the stage of development of the fungi, 10.22% (n = 14) of the infected ants had recently been killed (Fresh); 30.66% (n = 42) had stroma of the parasite (Stroma); 30.66% (n = 42) contained mature sexual fruiting bodies (Mature) and 28.47% (n = 39) were in the stroma or mature stages, but parasitized by more than one type of fungus (Hyperparasitized).

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Figure 1 – The death grip of *Camponotus renggeri* on the leaf's abaxial face (A) and approximate view of the host ant infected by *Ophiocordyceps camponoti-renggeri* with mycelium and fruiting body of the parasite. Source: Emily O. Fonseca.

In the subsequent expedition, 73 infected ants were found. Of the total number of parasitized individuals, the majority (79.45%, n = 58) were found in leaves of trees. Infected ants were also found in climbing vegetation (12.33%, n = 9), in young trees (6.85%, n = 5) and in a monocot species (1.37%, n = 1). The dead individuals of parasitized ants were invariably found on the leaves of the plants (100%, n = 73), often located on the abaxial face of this vegetative organ (97.26%, n = 71) especially close to the leaf apex (Fig. 1A). A single specimen was found on the adaxial side (1.37%) and another on the recombinant leaf rake. All individuals located on the abaxial and adaxial faces of the leaves were adhered by the mandibles to the margins or to the central rib of the leaf. There was a higher frequency of individuals adhering to the margins (79.45%, n = 58) than to the central ribs of the leaves (19.18%, n = 14).

As for the size of the leaves used for ant's fixation, there was a large variation in size (4.3 cm to 30.4 cm between the apex and the junction with the petiole), with an average size of 14.1 cm. Most ants died on simple phyllotaxis leaves (98.63%, n = 72), with a single individual being observed on a recomposed leaf. Regarding the height at which the parasitized ants died, a considerable variation was observed (76 cm to 2.18 m above the ground), with an average height of 1.5 m. Zombie ants were found between 1 to 4 leaves per tree, with an average of 1.55 leaves with zombie ant per host tree.

Discussion

The relatively large number of parasitized ants reported in this study reveals that the collection area constitutes a climatically favorable environment for the establishment of parasitic associations between the parasitic fungus *Ophiocordyceps camponoti-renggeri* and hosts *Camponotus renggeri*. Given that the relatively constant conditions of high humidity and temperature in tropical forests are ideal prerequisites for fungal infection (Evans, 1974; Andriolli et al., 2019), the Serra de Baturité has ideal conditions for the establishment of parasitic relationships of the fungus-ant type given its climate and high rates of parasitism in other taxa (PDITS, 2008; Sobczak et al., 2017b, 2019, 2020).

The most infected ant workers (69.35%) had recently been killed (fresh), had stroma (stroma) or were parasitized by other fungi (hyperparasitized), while only 42 specimens (30.66%) contained sexually fruiting mature bodies, capable of producing spores and effectively dispersing them. This pattern of higher proportions of fresh dead-ants coincides precisely with the region's rainy season, a pattern that is seen for parasitized *Camponotus atriceps* and *C. bispinosus* that were more abundant in periods with greater air humidity (Cardoso-Neto et al., 2019). This shows that, although the number of parasitic ants was high, most of these individuals were in a stage of life whose risk of infection for the rest of the colony was low. Similar results were obtained by Andersen et al. (2012) in a study on the interaction dynamics between *Ophiocordyceps* and its host ants. Other studies have found that, due to hyperparasitism, the fruiting bodies of *Ophiocordyceps* fungi are unable to release their spores, thereby reducing the impacts caused on *Camponotus* populations (Andersen et al., 2012; Araújo et al., 2018). Because ants contribute about 25% of animal biomass in tropical forests (Schultz, 2000), entomopathogenic fungi occupied an ecological niche little explored by other living beings. Thus, it is observed that hyperparasitic fungi perform the population control of *Ophiocordyceps* and guarantee the permanence of *Camponotus* colonies in the tropical forests of the world (Morozov et al., 2007; Andersen et al., 2012; Araújo & Hughes, 2016).

The frequent presence of dead ants fixed on the leaf margins close to the apex was also observed by Araújo et al. (2015) in a study that described three new species of specific *Camponotus* hosts on the fungus *Ophiocordyceps* in the Brazilian Amazon. This result, however, differs from those demonstrated by Sobczak et al. (2017) and Andersen et al. (2009) in which the authors observed a higher frequency of individuals adhering to the central ribs in relation to those fixed to the margins. The adaptation of death in the vicinity of the leaf apex can be explained by the dew drops formed on these tips throughout the year, thus enabling the continuous and consistent development of fungi (Araújo et al., 2015). It is also noteworthy that the choice of the host plant ant is not selective, but based mainly on environmental factors of temperature and humidity favorable to the development, close to the soil, of the parasitic fungus (Andersen et al., 2009; Andriolli et al., 2019). The strategic position of death of the parasitized ant (upside down) facilitates the release and deposition of fungal spores on the forest floor, which subsequently infect other ants that pass through (Araújo et al., 2015).

The observed frequency of ants parasitized at heights above the ground ranging from 76 cm to 2.18 m (mean = 1.5 m) is similar to other observations made in the locality (Sobczak et al., 2017). In contrast, in other studies of *Ophiocordyceps* parazited ants *Colobopsis leonardi* (Emery, 1889) was recorded very close to the ground, at an average height of 25.20 cm (Andersen et al., 2009). The authors suggest that lower heights provide more favorable conditions for the development of the parasite. This fact can be seen in a study made in Amazon Forest that demonstrate that *Camponotus (Myrmothrix) atriceps* (Smith, 1858) parasitized by *Ophiocordyceps camponoti-atricipis* can be found in higher areas in raised environments than at the forest edge, where light is available from lower layers (Andriolli et al., 2019). The preference for higher heights, however, may occur due to the type and structures provided by the plant species used for the death grip (Sobczak et al., 2017).

Camponotus is a frequent and diverse genus in neotropical regions, with many key species in processes and interactions, many of which are still unknown or with unknown distribution and life history (Santos-Silva et al., 2016, Vicente et al., 2016, 2018, 2019; Dáttilo et al., 2020; Jory & Feitosa, 2020). In addition, the diversity of parasites that can lead to this behavior and the frequency with which it happens is still superficially studied.

Conclusion

This study brings essential information about the natural history of the fungus, as well as the dynamics of the fungus. Knowing aspects of the life history of the organisms involved in the relationship can help to understand the dynamics of parasitism and can contribute with biological control programs.

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References

Alves SB. 1988. Fungos entomopatogênicos. In: Alves SB (ed.), Controle microbiano de insetos (p. 308-310). 2.ed. Piracicaba: FEALQ.

Andersen SB, Ferrari M, Evans HC, Elliot SL, Boomsma JJ, Hughes DP. Disease dynamics in a specialized parasite of ant societies. PloS ONE 7. 2012; e36352. doi: 10.1371/journal.pone.0036352

Andersen SB et al. The life of a dead ant: the expression of an adaptive extended phenotype. The American Naturalist. 2009; 174: 424-433. doi: 10.1086/603640

Andrade CFS. Epizootia natural causada por *Cordyceps unilateralis* (Hypocreales, Euascomycetes) em adultos de *Camponutus* sp. (Hymenoptera, Formicidae) na região de Manaus, Amazonas, Brasil. Acta Amazonica. 1980; 10: 671-677. doi: 10.1590/1809-43921980103671

Andriolli FS, Ishikawa NK, Vargas-Isla R, Cabral TS, Bekker C, Baccaro FB. Do zombie ant fungi turn their hosts into light seekers? Behavioral Ecology. 2019; 30: 609-616. doi: 10.1093/beheco/ary198

Antmaps. <https://antmaps.org>. Access on: 03/10/2021.

Antweb. <http://www.antweb.org>. Access on: 03/10/2021.

Araújo JPM, Evans HC, Geiser DM, Mackay WP, Hughes DP. Unravelling the diversity behind the *Ophiocordyceps unilateralis* (Ophiocordycipitaceae) complex: Three new species of zombie-ant fungi from the Brazilian Amazon. Phytotaxa. 2015; 220: 224-238. doi: 10.11646/phytotaxa.220.3.2

Araújo JPM, Evans HC, Kepler R, Hughes DP. Zombie-ant fungi across continents: 15 new species and new combinations within Ophiocordyceps. I. Myrmecophilous hirsutelloid species. Studies in Mycology. 2018; 90: 119-160. doi: 10.1016/j.simyco.2017.12.002

Araújo JPM, Hughes DP. Diversity of Entomopathogenic Fungi: Which groups conquered the insect body? In: Lovett B, Leger RS. Genetics and molecular biology of entomopathogenic fungi. Academic Press; 2016.

Basset Y *et al*. Arthropod diversity in a tropical forest. Science. 2012; 338: 1481-1484. doi: 10.1126/science.1226727

Brandão CRF. Adendos ao catálogo abreviado das formigas da região Neotropical (Hymenoptera: Formicidae). Revista Brasileira de Entomologia. 1991; 35: 319-412. doi: http://doi.org/10.5281/zenodo.24565

Cardoso-Neto JAC, Leal LC, Baccaro FB. Temporal and spatial gradients of humidity shape the occurrence and the behavioral manipulation of ants infected by entomopathogenic fungi in Central Amazon. Fungal Ecology. 2019; 42: 100871. https://doi.org/10.1016/j.funeco.2019.100871

Cooke RC, Whipps JM. The evolution of modes of nutrition in fungi parasitic on terrestrial plants. Biological Reviews. 1980; 55: 341-362. doi: 10.1111/j.1469-185X.1980.tb00697.x

Dáttilo W et al. Mexico ants: incidence and abundance along the Nearctic–Neotropical interface. Ecology. 2020; 101: e02944. doi: 10.1002/ecy.2944

Dawkins R. The extended phenotypes: The gene as the unit of selection. Oxford: Oxford University Press, 307p, 1982.

Delgado PAM, Murcia OP. Hongos entomopatógenos: uma alternativa para la obtención de Biopesticidas. Ambi-Agua 6: 77-90, 2011. doi: 10.4136/ambi-agua.187

Evans HC. Natural control of arthropods, with special reference to ants (Formicidae), by fungi in the tropical high forest of Ghana. Journal of Applied Ecology. 1974; 11: 37-49. doi: 10.2307/2402003

Hawksworth DL. The magnitude of fungal diversity: the 1.5 million species estimate revisited. Mycological research. 2001; 105: 1422-1432. doi: 10.1017/S0953756201004725

Hawksworth DL, Lücking R. Fungal diversity revisited: 2.2 to 3.8 million species. The fungal kingdom 79-95, 2017. doi: 10.1128/microbiolspec.FUNK-0052-2016

Hughes DP. Pathways to understanding the extended phenotype of parasites in their hosts. Journal of Experimental Biology. 2013; 216(1): 142-147. doi: 10.1242/jeb.077461

Hughes DP, Libersat F. Parasite manipulation of host behavior. Current Biology. 2019; 29: 45-47. doi: 10.1016/j.cub.2018.12.001

Hughes DP, Andersen SB, Hywel-Jones NL, Himaman W, Billen J, Boomsma JJ. Behavioral mechanisms and morphological symptoms of zombie ants dying from fungal infection. BMC ecology. 2011; 11(1): 13. doi: 10.1186/1472-6785-11-13

Janicki J, Narula N, Ziegler M, Guénard B, Economo EP. Visualizing and interacting with large-volume biodiversity data using client-server web-mapping applications: The design and implementation of antmaps.org. Ecological Informatics. 2016; 32: 185-193. doi: 10.1016/j.ecoinf.2016.02.006

Khachatourians GG, Qazi SS. Entomopathogenic fungi: biochemistry and molecular biology. 2008. In: Brakhage AA, Zipfel PF (eds.). Human and animal relationships. Springer, Berlin, Heidelberg, 296p.

Loreto RG, Elliot SL, Freitas ML, Pereira TM, Hughes DP. Long-term disease dynamics for a specialized parasite of ant societies: a field study. PloS ONE. 2014; 9: e103516. doi: 10.1371/journal.pone.0103516

Maccheroni W, Araújo WL, Lima AOS. 2004. Fungos: uma introdução à biologia, bioquímica e biotecnologia. Caxias do Sul: EDUCS, 490p.

Mora MAS, Castilho AMC, Fraga ME. Classification and infection mechanism of entomopathogenic fungi. Arquivos do Instituto Biológico. 2017; 84: 1-10. doi: 10.1590/1808-1657000552015

Moro MF, Macedo MB, Moura-Fé MMD, Castro ASF, Costa RCD. Vegetação, unidades fitoecológicas e diversidade paisagística do estado do Ceará. Rodriguésia. 2015; 66: 717-743. doi: 10.1590/2175-7860201566305

Morozov AY, Robin C, Franc A. A simple model for the dynamics of a host–parasite–hyperparasite interaction. Journal of theoretical biology. 2007; 249: 246-253. doi: 10.1016/j.jtbi.2007.05.041

Nascimento FR, Souza MJN. Diagnóstico Socioeconômico da Área de Proteção Ambiental da Serra de Baturité/Ceará. Raega – O Espaço Geográfico em Análise. 2010; 20: 19-33. doi: 10.5380/raega.v20i0.20602

PDITS. 2008. Plano de Desenvolvimento Integrado do Turismo Sustentável: Polo Maciço de Baturité. Fortaleza/CE, 129p.

Prado LP, Feitosa RM, Triana SP, Gutiérrez JAM, Rousseau GX, Silva RA et al. An overview of the ant fauna (Hymenoptera: Formicidae) of the state of Maranhão, Brazil. Papéis Avulsos de Zoologia. 2019; 59: e20195938. doi: 10.15560/12.4.1922

Rebouças NC, Sila Aivy AF, Sousa LM. Vascular epiphytes (Spermatophytes) of the Baturité Massif, Ceará, Northeast Brazil. Revista Brasileira de Geografia Física. 2021; 14(03), 1748-1766.

Santos-Silva L, Vicente RE, Feitosa RM. Ant species (Hymenoptera, Formicidae) of forest fragments and urban areas in a Meridional Amazonian landscape. Check List. 2016; 12: 1885. doi: 10.15560/12.3.1885

Schultz TR. In search of ant ancestors. Proceedings of the National Academy of Sciences. 2000; 97: 14028-14029. doi: 10.1073/pnas.011513798

Shrestha B, Tanaka E, Hyun MW, Han JG, Kim CS, Jo JW et al. Coleopteran and lepidopteran hosts of the entomopathogenic genus *Cordyceps* sensu lato. The Journal of Mycology. 2016; 2016: 1-16. doi: 10.1155/2016/7648219

Silva-Viana CB, Vicente RE, Kaminski LA, Izzo TJ. Beyond the gardens: The extended mutualism from ant-garden ants to nectary-bearing plants growing in Amazon tree-fall gaps. Biotropica. 2021; 53(2), 433-441.

Sobczak JF, Arruda IDP, Pádua DG, Villanueva-Bonilla GA. Parasitism in *Theridion* sp. (Araneae: Theridiidae) by *Zatypota riverai* Gauld, 1991 (Hymenoptera: Ichneumonidae: Pimplinae). The Journal of Arachnology. 2019; 47: 266-270. doi: 10.1636/JoA-S-18-103

Sobczak JF, Arruda IDP, Fonseca EO, Rabelo PJQ, Julião P, Nóbrega S et al. Manipulation of Wasp (Hymenoptera: Vespidae) Behavior by the Entomopathogenic Fungus *Ophiocordyceps humbertii* in the Atlantic Forest in Ceará, Brazil. Entomological News. 2020; 129(1): 98-104. doi: 10.3157/021.129.0115

Sobczak JF, Costa LFA, Carvalho JLVR, Salgado-Neto G, Moura-Sobczak JCMS, Messas YF. The zombie ants parasitized by the fungi *Ophiocordyceps camponoti-atricipis* (Hypocreales: Ophiocordycipitaceae): new occurrence and natural history. Mycosphere. 2017; 8: 1261-1266. doi: 10.5943/mycosphere/8/9/1

Sobczak JF, Pádua DG, Costa LF, Carvalho JL, Ferreira JPS, Sobczak J et al. The parasitoid wasp *Eruga unilabiana* Pádua & Sobczak, sp. nov. (Hymenoptera: Ichneumonidae) induces behavioral modification in its spider host. Entomological Science. 2017; 21: 59-65. doi: 10.1111/ens.12278

Vicente RE, Izzo TJ. Effect of dominant parabiotic Ant-Garden ants on the understory and ground-dwelling ant assemblage in the Amazon rainforest. Insect Conservation and Diversity. 2021; 14: 95-106. doi: 10.1111/icad.12449

Vicente RE, Ferreira AC, Santos RCLD, Prado LPD. Ants (Hymenoptera: Formicidae) from an Amazonian fragmented landscape, Juara, Mato Grosso, Brazil, with new records of ant species. Papéis Avulsos de Zoologia. 2018; 58: e20185840. doi: 10.11606/1807-0205/2018.58.40

Vicente RE, Ferreira-Silva D, Guerreiro LM. New records of three Neotropical arboreal ant species of *Camponotus*, subgenus Dendromyrmex (Hymenoptera: Formicidae) for the southern Amazon, including biological information. Acta Amazonica. 2019; 49(1): 36-40. doi: 10.1590/1809-4392201801951

Vicente RE, Prado LP, Izzo TJ. Amazon rainforest Ant-Fauna of Parque Estadual do Cristalino: understory and ground-dwelling Ants. Sociobiology. 2016; 63: 894-908. doi: 10.13102/sociobiology.v63i3.1043

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