



When zombies go vegan: *Ophiocordyceps unilateralis* hosts are selecting to bite palm leaves before dying?

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ABSTRACT

Some parasites that modify hosts' behavior can receive reproductive advantages. For instance, when infected by *Ophiocordyceps unilateralis* s.l., ants climb understory plants, lock their jaws into the plant tissue, and die in stable microclimatic conditions that favor the reproductive stage of the fungus. However, the so-called "zombie ants" could die on different species of plants, subject to varying environmental pressures. Here, we investigated whether infected ants lock their jaws on particular species of understory plants more often than expected before dying from the infection. We hypothesize that there may be different reproductive advantages to the parasite based on the plant species on which its hosts die. Our findings reveal that 36.3% of the infected ants died on palm trees, specifically *Attalea* sp. and *Euterpe catinga*, more frequently than expected by chance. Also, we found that cadavers tend to persist longer on palms than other plants. Our results suggest that there may be a reproductive advantage for the parasite when its hosts die on palm leaves. Palms generally have long leaf durability, which can reduce parasite cadaver loss by foliar abscission and increase cumulative spore dispersal. Furthermore, we propose abundant plant species with no observance of cadavers potentially have traits like trichome coating and antifungal compounds that may influence the arrival and permanence of new zombie ants. Our results show that infected ants dying on certain understory palm species may increase the fungus' fitness.

1. Introduction

Some specialized parasites can favor your reproduction and dispersal by modifying the behavior of their hosts (Thomas et al., 2010). These behavioral changes expressed by the host phenotype are known as adaptive extensions of the parasite genes (Dawkins, 1982). The extended phenotype hypothesis suggests that these modifications are fine-tuned traits that increase the parasite's fitness (Dawkins, 1982; Moore et al., 2005). For instance, uninfected caterpillars avoid higher ground forest places during the day where they are most visible to possible predators such as birds (Hoover et al., 2011; Han et al., 2018; Ros et al., 2015). However, caterpillars infected by baculovirus climb to

the top of trees and shrubs and die in a liquefied state, which spreads the virus to other caterpillars below (Goulson, 1997). Crickets parasitized by nematomorphs often drown by jumping into bodies of water, where the parasite leaves the host as part of its life cycle. Crickets without these parasites avoid risky aquatic habits (May, 1920; Ponton et al., 2011; Thomas et al., 2002). Cicadas infected by the fungus of the *Massospora* genus have their abdomens transformed into masses of infective spores, displaying hypersexual behavior. Infected cicada males will display female mating behaviors and copulate with other males, spreading the infection to new hosts without transferring genetic material (Cooley et al., 2018; Han et al., 2018; Speare, 1921). These coevolutionary examples highlight the need for more studies to understand better the

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relationship between parasites and the phenotypic modifications of their hosts (Poulin and Thomas, 1999).

The ants of the Camponotini Tribe (Formicinae: Formicidae) infected by the fungus *Ophiocordyceps unilateralis sensu lato* (Hypocreales: Ophiocordycipitaceae) exhibit typical extended phenotype traits (Andersen et al., 2009). Infected ants climb understory plants like small trees and bushes with erratic and trembling walking patterns before locking their jaws onto vegetal tissue (Evans and Samson, 1984; de Bekker et al., 2015; Hughes et al., 2011). These locations may present optimal microclimatic conditions for the parasite's reproductive stage (Andersen et al., 2009; Andriolli et al., 2019; Cardoso Neto et al., 2019; Chung et al., 2017; Evans and Samson, 1984; Hughes et al., 2011). A few weeks after the ant locks its jaw onto a plant tissue, the fungus develops a fruiting body and releases spores that may reach uninfected ants and spread the disease to new hosts (de Bekker et al., 2015; Evans et al., 2011). This set of infection characteristics and changes in behavior made these hosts known as zombie ants (Andersen et al., 2009; Evans and Samson, 1982, 1984). Additionally, the *O. unilateralis s.l.* complex species show evidence of a specific relationship with respective host species (Araújo et al., 2018; Evans et al., 2011; Kobmoo et al., 2012; Sakolrak et al., 2018).

The behavioral changes of ants infected by *O. unilateralis s.l.* may represent traits related to microclimate and microhabitat selection, which is still not completely understood (Andersen et al., 2009; Andriolli et al., 2024). These environmental pressures may provide variable evolutionary pathways for extended phenotypes in host species (Andersen et al., 2009; Evans et al., 2011; Loreto et al., 2018; Will et al., 2022). For example, one study found that most ants infected with *O. unilateralis s.l.* in tropical forests bite understory leaves before dying (Andersen et al., 2009). In temperate forests, on the other hand, ants tend to bite twigs before dying from *Ophiocordyceps* infection (Loreto et al., 2018). The parasitized ants that lock their jaws on leaves in deciduous forests may not achieve the reproductive phase during the temperate fall season through the leaf abscission. In this context, differential reproductive success for the parasite depends on the substrate in which infected ants perish, with sturdier substrates allowing ample time for the parasite to grow and spread its spores (Andriolli et al., 2024). While the cadaver remains mummified on the substrate, the fungus can produce more than one fruiting body (iteroparity), enhancing the spores released into the environment (Andersen et al., 2012; Evans and Samson, 1982; Mongkolsamrit et al., 2012).

The understory of tropical forests is a shaded environment, and emerging plants and shrubs can present adaptive responses to low available light (Chazdon and Fetcher, 1984; Chazdon, 1986). For example, understory plants may present slow vegetative growth in juveniles compared to adults, and some species may prolong the leaf life span as a shading strategy response (Kikuzawa, 1991). Palm leaves in tropical forests often exhibit remarkable longevity, lasting more than five years in some species (Cunningham, 1997). These palms, especially the juvenile stage, are adapted to the shaded competitive understory environment (Ataroff and Schwarzkopf, 1992). In this way, these plants can maximize the leaf lifetime and enable efficient resource utilization by prioritizing the biomass for the leaves during the pre-reproductive period (Ataroff and Schwarzkopf, 1994). Thus, the likelihood of successful *O. unilateralis* reproduction and spore release may be increased when infected ants bite long-life leaves by reducing cadaver losses due to foliar abscission and enabling new fruiting bodies via iteroparity (Mongkolsamrit et al., 2012).

In this study, we suggest that the parasite benefits from reproductive success when hosts lock their jaws and die on certain understory plants. We hypothesize that plants with long leaf durability, like palms, may reduce cadaver loss, sheltering more cadavers. To investigate this, we conducted a field study focused on sampling the understory plants, where we identified which plant species we found carpenter ants infected with *O. unilateralis s.l.* In addition, we used a large dataset that monitored the ant cadavers for approximately a year in an Amazonian

central forest (Cardoso Neto et al., 2019) to inspect how long the *Camponotus*-infected zombie ants can last on palms and other plant leaves.

2. Methods

2.1. Study area

We carried out this study in the Cuieiras River Biological Reserve (reference geographical coordinates: 2°35.37S, 60°06.92 W) of the Instituto Nacional de Pesquisas da Amazônia (INPA), located ~ 60 km North of Manaus, Amazonas state, Brazil. The reserve is located in the lower Rio Negro basin and covers 22,735 ha (Marques Filho et al., 2005). The primary vegetation of the region is a habitat mosaic with trees reaching 35–40 m, composed of Terra-firme (upland forest), Campinarana (white sand transitional forest), and a periodically black water-flooded vegetation called Igapó (Adeney et al., 2016; Junk et al., 2011; Prance, 1978).

2.2. Experimental design

We searched for infected dead ants in shrubs and small trees at ~2 m in height on the trails around the Reserve INPA's base in August 2014. When we found a zombified ant, we inspected the four nearest plants that measured higher than 50 cm in height in each cardinal direction around the focal plant (Fig. 1). For every localized zombie ant, we identified the focal plant (i.e., the plant where we found the first ant) and the four closest plants. If there were zombie ants in any of the four neighboring plants inspected, we recorded this information but did not then use these plants as focal plants for a new sample. Focal plants were at least 50 m apart from each other. We used this approach to obtain a representative sample of plant species around the central plant in the search for zombie ants.

We identified plants at the highest possible taxonomic level. Sterile samples of the plants were collected and compared with the specimens deposited in the INPA (Instituto Nacional de Pesquisas da Amazônia) herbarium. We standardized the plant names according to the species list following the Brazilian Flora database (Flora e Funga do Brasil, 2024). We also collected ant cadaver samples for further identification. Additionally, we used part of a dataset that monitored dead infected ants for approximately a year in the Ducke Reserve, Amazonas state, Brazil (see Cardoso Neto et al., 2019 for details) to investigate how long *Camponotus* cadavers infected with *O. unilateralis s.l.* can spend on palms or other plant leaves.

2.3. Data analysis

We used chi-squared tests to investigate if the frequency of encountering infected ants on certain species is higher than expected by chance among the plants most commonly encountered in our sampling. We tested this at the family and species levels and only for plant families and species with at least four individuals presenting zombie ants. We also applied chi-squared tests between more common plant species that we found without cadavers during our fieldwork. Additionally, we used survival analyses (log-rank test) to inspect whether ant cadavers are maintained longer on palm leaves versus other plants. To conduct this analysis, we considered only the *O. unilateralis s.l.* hosts (*Camponotus* ants) in the Cardoso Neto et al., (2019) dataset. We performed all statistical analyses in the software R (R Core Team, 2021) with the package's 'survival' (Therneau, 2021), 'survminer' (Kassambara et al., 2018), and 'ggplot2' (Wickham, 2016) to build graphics.

3. Results

We identified 32 understory plant families and 18 with ant cadavers. Arecaceae family (47 individuals), Burseraceae (36 individuals), and



Fig. 1. Sample representation of the field-collected data. The figure shows the focal plant (F) with detected zombie ants. The red square shows a detailed zombie *Camponotus atriceps* and the four proximal plants (>50 cm) around the focal plant that we searched for new zombie ants in cardinal directions. N- north plant, S- south plant, E- east plant, and W- west plant. Zombie ant wash-drawing by Hadna Abreu. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Euphorbiaceae (19 individuals) were the most common families found with dead ants (Fig. 1). Moreover, Chrysobalanaceae (8) and Myristicaceae (6) were representative families found without zombie ants. The chi-squared test results between the plant families showed that only Arecaceae had more dead ants than expected by chance ($p = 0.004$, Table 1).

We identified 105 plant species (or morphotyped species), and 35 (33.3%) showed ant cadavers infected with *O. unilateralis* s.l. At the species level, *Attalea* sp. and *Euterpe catinga*, both Arecaceae, had more dead ants than expected by chance (Table 2., $p < 0.001$ and $p = 0.046$, respectively). We found no significant difference in the chi-squared results between the species most frequently found without cadavers: *Psychotria pacimonica* (9 individuals, Rubiaceae, chi-squared = 2.778, $p = 0.127$), *Iriartella setigera* (7 individuals, Arecaceae, chi-squared = 2.165, $p = 0.201$), *Iryanthera ulei* (6 individuals, Myristicaceae, chi-

Table 1
Chi-squared test results of the most numerous understory plants at the family level with dead infected ants.

Family	Chi-squared	p-value
Annonaceae	0.003	1
Arecaceae	8.20	0.004
Burseraceae	0.04	1
Calophyllaceae	0.006	1
Dichapetalaceae	0.003	1
Euphorbiaceae	1.76	0.27
Fabaceae	2.35	0.19
Lauraceae	1.02	0.46
Myrtaceae	0.70	0.51
Rubiaceae	0.06	1
Sapotaceae	0.006	1

Table 2
Chi-squared test results of the most numerous understory plant species found with cadavers.

Family	Specie	Chi-squared	p-value
Arecaceae	<i>Attalea</i> sp.	13.82	>0.001
Arecaceae	<i>Euterpe caatinga</i>	4.22	0.046
Arecaceae	<i>Bactris</i> sp.	0.43	0.68
Burseraceae	<i>Protium crassipetalum</i>	0.003	1
Burseraceae	<i>Protium paniculatum</i>	0.32	0.74
Dichapetalaceae	<i>Tapura lanceolata</i>	0.01	1
Calophyllaceae	<i>Caraipa</i> sp.	0.86	1
Euphorbiaceae	<i>Pausandra macropetala</i>	1.27	0.31
Myrtaceae	<i>Myrciaria</i> sp.	3.48	0.10
Sapotaceae	<i>Pouteria eugenifolia</i>	0.43	0.68

squared = 1.858, $p = 0.316$), *Elaeoluma nuda* (6 individuals, Sapotaceae, chi-squared = 1.858, $p = 0.349$) and *Protium opacum* (5 individuals, Burseraceae, chi-squared = 1.550, $p = 0.359$).

We found 77 dead ants and six species infected with *O. unilateralis* s.l. *Camponotus atriceps* was the most commonly infected species (64), representing 83.1%. The other species found infected were *Camponotus bidens* (2), *Camponotus crassus* (2), *Camponotus chartifex* (1), and the morphotype *Camponotus* sp. (4) and *Camponotus* sp. 2 (4). We found 28 ants (36.4%) in palm trees (Arecaceae, Table 3), 12 were on *Attalea* sp., 11 on *Euterpe catinga*, four on *Bactris* sp., and one ant on *Oenocarpus bataua*. The family with the second highest number of ant cadavers found was Annonaceae, with nine dead ants, followed by eight ants found in Burseraceae.

Among the 77 ant cadavers that we sampled, 52 individuals (67.5%) show decay characteristics (i.e., parched ants presenting loss of

Table 3
Number of cadavers encountered by understory plant family.

Number of cadavers	Individuals	Family
28	47	Arecaceae
8	36	Burseraceae
3	19	Euphorbiaceae
1	15	Fabaceae
4	15	Rubiaceae
5	15	Myrtaceae
5	15	Sapotaceae
9	13	Annonaceae
2	10	Lauraceae
2	9	Dichapetalaceae
2	8	Calophyllaceae
1	4	Moraceae
2	2	Araceae
1	2	Clusiaceae
1	2	Humiriaceae
1	2	Malvaceae
1	1	Salicaceae
1	1	Streliziaceae

appendages and, when present, dark and opaque fruiting bodies). Of the 52 old cadavers, 20 were biting juveniles of palm trees (Arecaceae). Also, we found 19 mature or growing fungus fruiting bodies (presenting vivid light brown color), the majority (14) emerging from *C. atriceps* species (Fig. 2).

The survival analyses (dataset of Cardoso Neto et al., 2019) show that the *Camponotus* cadavers tend to last more time adhered onto palms than other plant leaves (log-rank test: $p < 0.001$). Cadavers on palm trees had a median permanence of ~185 days, while other understory plants presented ~125 days attached to plant substrate (Fig. 3).

4. Discussion

Our results revealed that zombie ants infected with *O. unilateralis* seem to die more frequently on certain understory plant species. More than a third of them locked their jaws on the leaves of juvenile palm trees, the only family (Arecaceae) and species (*Attalea* sp. and *Euterpe catinga*) that presented more cadavers than expected by chance. Moreover, our results suggest that the leaves of understory palms where the hosts have a solid fix and stable microclimatic conditions seem to increase the parasites' reproductive performance (Andersen et al., 2009;

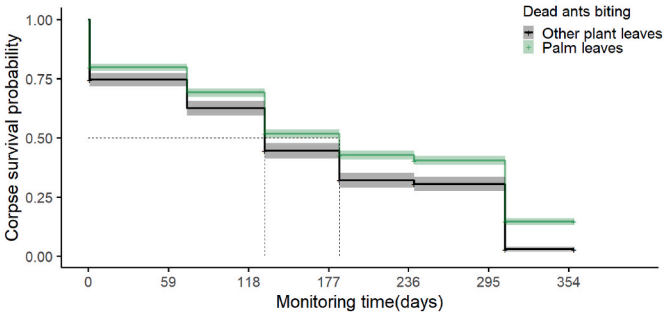


Fig. 3. Survival curves of carpenter zombie ants that bite palms or different understory plant leaves (data from Cardoso Neto et al., 2019). The median survival shows ~185 days for cadavers in palm leaves and ~125 days for other plant leaves.

Loreto et al., 2018). In addition, the survival analyses show that the *Camponotus* sp. hosts of *O. unilateralis* attached to palm leaves remained on them for about 60 days longer than on other understory plants. That additional time minimizes the loss of the hosts and likely enhances the parasite's life cycle propagation (Andriolli et al., 2024). We further suggest that the platform-like orientation of some of the palm leaf species which may facilitate the dispersion of the spores, is enhanced by the presence of leaflets (compound leaves), increasing the surface area where the zombie ants can bite.

Amazonian plant abundance has concentrated in a relatively few hyper-dominant species, with a disproportionate number of Arecaceae, Myristicaceae, and Lecytidaceae families. Furthermore, six of the 10 most common and abundant plant species in the Amazon are palms (Ter Steege et al., 2013). We found most zombie ants on abundant understory plants. However, *Iriartella setigera* (Arecaceae) and *Iryanthera ulei* (Myristicaceae), which are hyper-dominant species in the Amazon, did not present cadavers (Ter Steege et al., 2013). The abundant plants encountered without cadavers may have characteristics that distinguish them from those that show plenty of hosts. We propose that plants without cadavers may have morphological traits that may hinder the attachment of zombie ants and chemical compounds that may potentially interfere with the parasite reproductive cycle.

The species *Iriartella setigera* presents a trichome coating on all leaf structures (Flora e Funga do Brasil, 2024). The trichomes can make it



Fig. 2. *Camponotus atriceps* biting understory plants. The white arrows indicate the parasite's fruiting body stage. a- A growing fruiting body with the ant biting the terminal region of a leaf. b- A mature fruiting body with the ant biting the apical extension of a palm leaflet (Arecaceae). c- An example of a fresh light brown fruiting body. d- A typical older and dry dark brown fruiting body. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

difficult for ants to reach the leaf and lock their jaws, intensified by their trembling gait at this infection stage (Andersen et al., 2009). Additionally, the leaves of this species lack the apical extension of the leaflet, where many zombie ants usually arrive before death. *Iryanthera ulei* has coriaceous leaves without trichomes, which are thick and rigid and may have recurved leaf margins. Despite not having trichomes, thick and curved leaf margins can make it difficult for ants to lock their jaws. Latex is also a typical characteristic of this genus (Roosmalen et al., 1996). Latex leaks may decrease the friction between the leaf and the mandibles, making it difficult for the host to attach. Thus, these are some physical traits of plants that can mechanically hinder the arrival of the ants. Besides that, *Iryanthera* species present antifungal properties, having been used by indigenous people to treat fungal infections and to clean infected wounds (Gottlieb, 1979; Schultes and Holmstedt, 1971). We suggest that the antifungal compounds of these plants, possibly present in the latex, could make the parasite's reproductive phase unfeasible, even if an infected ant could fix its jaws onto these leaves before dying. Thus, the morphological leaf traits and the chemical substances may account for the absence of zombie ants on these plants and could help explain our findings.

Other representative plant species that we found without ants are *Psychotria pacimonica* (Rubiaceae), *Elaeoluma nuda* (Sapotaceae), and *Protium opacum* (Burseraceae). *Psychotria* is the most diverse genus within Rubiaceae, a commonly encountered family in the understory of tropical forests (Hamilton, 1989). Plants in this genus present a series of chemical compounds with antifungal properties like coumarins and diterpenes (Benevides et al., 2005). The species *E. nuda* (Sapotaceae) and *P. opacum* (Burseraceae) are also abundant in the understory of tropical forests and have exudates that present antifungal properties (Baky et al., 2016; Rüdiger et al., 2007). In this regard, these findings suggest that it may be adaptative and aid in fungal reproduction when infected ants bite plant species that do not have potential antifungal properties.

Our study shows that the abundance of the understory plants alone cannot explain the presence of *Ophiocordyceps*-infected ant cadavers. Our findings suggest that some species of palms seem to have traits, such as long-lived leaves, which can enhance the fungus' survival. We propose that some mechanical and chemical characteristics in plants where fewer or no zombie ants may deter ants from reaching or dying on their leaves. Therefore, several plant species commonly found in the understory may have traits that can preclude the *O. unilateralis* s.l. from completing its reproductive cycle, which may drive parasite selection in the opposite direction of these such plants.

CRediT authorship contribution statement

Fernando S. Andriolli: Writing – review & editing, Writing – original draft, Data curation. **J. Aragão Cardoso Neto:** Writing – review & editing, Data curation. **Paul V.A. Fine:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Conceptualization. **Diego Salazar:** Writing – review & editing, Methodology, Investigation, Data curation. **Giovanna Figueroa:** Writing – review & editing, Investigation, Data curation. **Diego V. Torres:** Writing – review & editing, Investigation, Data curation. **J. Wellington de Morais:** Writing – review & editing, Supervision, Project administration, Investigation, Conceptualization. **Fabrizio B. Baccaro:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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