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SHORT COMMUNICATION

A natural history account of *Megalomyrmex ayri* Brandão, 1990 (Hymenoptera: Formicidae: Myrmicinae)

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Abstract

The ant genus *Megalomyrmex* Forel, 1885, has 45 valid species and is spread across the entire Neotropical region. *Megalomyrmex* species have been studied for decades and there are many rich natural history accounts that describe various details, including symbionts and unusual reproductive strategies. Natural history traits such as lifestyle have been used to help delimit *Megalomyrmex* species and the four species groups (i.e., Leoninus, Modestus, Pusillus, and Silvestrii), but recent findings suggest well-sampled comparative studies coupled with revisionary taxonomy are still needed. We report observations of the natural history of the *Megalomyrmex ayri* Brandão, 1990, regarding diet, nesting habits, abundance, distribution, and reproductive strategy. The sampling was conducted in a Terra Firme Forest, in the municipality of Itaituba, state of Pará, in the Tapajós River region of the Brazilian Amazon. Our observations reduce knowledge gaps about the lesser known *Megalomyrmex* species, and are essential for an understanding of the evolutionary history of the genus.

Keywords Ants · Behavior · Atlantic forest · Amazon · Brazil

Introduction

Natural history discoveries have contributed to broad applications in the fields of ecology, evolution, conservation, agriculture, and human health (Graham et al. 2004), but despite this, the natural history biology of most tropical species remain to be studied (Tschinkel and Wilson 2014). Inspired by Brandão (1990), who combined the natural history, morphology, and distribution data to diagnose the Neotropical ant genus *Megalomyrmex* species in four species groups (Leoninus, Modestus, Pusillus, and Silvestrii), additional descriptive studies continue to be outlined. Recent work has improved the understanding of evolutionary relationships within the genus, to characterize their diverse habits, and to identify the origins of symbiotic behaviors (e.g., Adams et al. 2000; Adams and Longino 2007; Boudinot et al. 2013; Sozanski et al. 2020).

Megalomyrmex has 45 extant species (Bolton 2021). The species within this genus exhibit great morphological diversity (e.g., size, color and sculpturation of the body surface) and a variety of nesting behaviors (e.g., underground, between leaves, under stones, within a host's nest), diet (e.g., insects, honeydew, fungal garden, brood), reproductive strategies (winged or wingless queens), social structure (monogynous or polygynous) (Boudinot et al. 2013), and alkaloid structural diversity (Adams et al. 2015). The genus includes both free-living species as well as social-parasitic species (thief ants, raiding agro-predator ants, and guest ants) that associate with fungus-farming ant hosts (Adams et al. 2012; Peeters and Adams 2016).

The four *Megalomyrmex* species groups have served well as hypotheses for further revisionary studies (Boudinot et al. 2013). As more and more species are described and the

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series of species previously known by only a few individuals and localities has increased, original traits proposed to be unique to the groupings (e.g., body size and reproductive strategy) are losing support (Boudinot et al. 2013). The inclusion of preliminary molecular data (Adams and Jones 2010), male morphology, and new behavioral data from species distributed in Central America further contributed to the understanding of the relationships between species groups, and to the taxonomic resolution of the species complex (Boudinot et al. 2013). However, taxonomic and behavioral data of species distributed in South America need to be integrated so that questions about the taxonomy and natural history of the species can be well-resolved.

Megalomyrmex ayri Brandão 1990, included originally in the Modestus species group, is a species with virtually unknown biology. It has a distribution throughout the Brazilian Amazon region, in Cerrado-Amazon ecotone, and in the northern portion of the Atlantic Forest (Brandão 2003). Due to the lack of natural history data and morphological similarities, *M. ayri* has been frequently confused with *M. goeldii* Forel 1912 in the literature and in museum collections. According to Brandão (1990), Walter Kempf indicated that *M. ayri* could be a new species by writing on the specimen determination label "*Megalomyrmex* pr. [near] *goeldii,* talvez [maybe] sp.n.". However, differences in the shape of the median portion of the clypeus—convex in *M. goeldii* and pointed in *M. ayri*—in addition to queen morphology, allow us to distinguish the two species (Brandão 1990).

In this paper, we provide detailed description of biological features of *M. ayri*. Our results include data on diet, nesting, abundance, distribution, and reproductive strategy. This work contributes to a better understanding of the natural history of *Megalomyrmex*, and increases our knowledge of species found in the Neotropical region.

Materials and methods

The sampling was conducted from January to February 2018, in a *Terra Firme* Forest, in the municipality of Itaituba, state of Pará, in the Tapajós River region of the Brazilian Amazonia (Figs. 1, 2a). Behavioral observations were

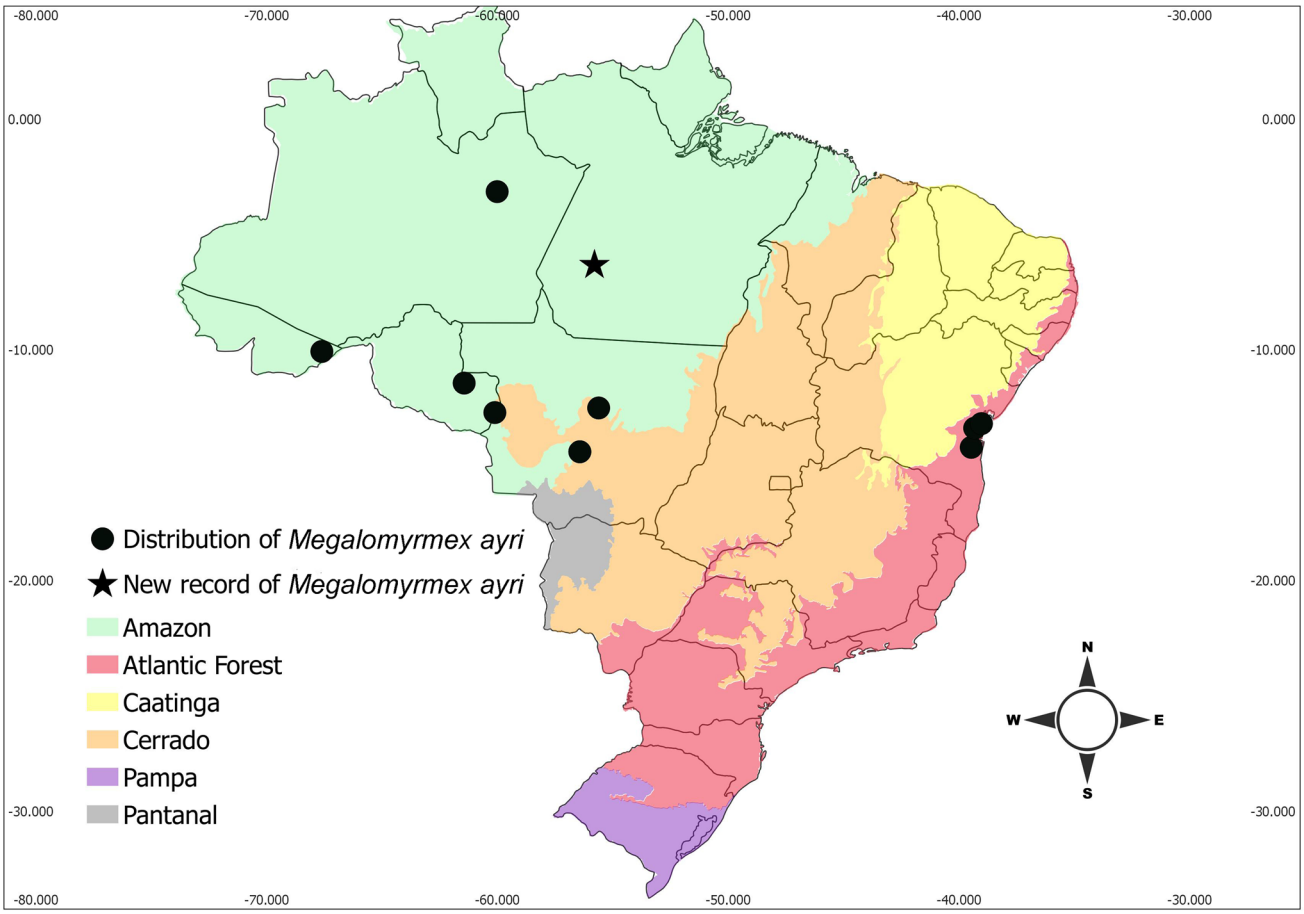

Fig. 1 Updated known distribution of *Megalomyrmex ayri*

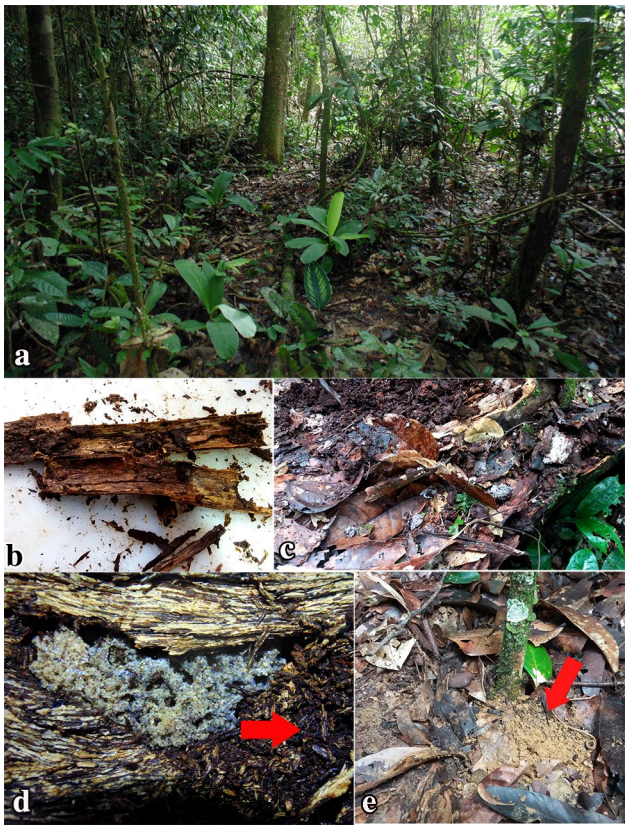

Fig. 2 **a** Collection site (Itaituba, Pará, Brazil). **b–e** Images of four of the five nests occupied by *Megalomyrmex ayri* recorded during fieldwork (all nests were photographed after colony removal); **b** colony recorded in a twig (colony #2); **c** colony recorded in a fallen log on the litter in a highly decomposed degree of decayed wood (colony #3); **d** colony recorded very close to the nest of the fungus-growing ant *Mycetophylax faunulus* (colony #4); **e** colony located in the ground (colony #5)

carried out during colony location and collection. During collection, three features of the *M. ayri* nests were recorded: (1) nest size (length in cm), (2) nest structure, and (3) the proximity of other ant species' nests. In the laboratory, we counted the number of individuals for each caste and sex (worker and queen), and immature (eggs, larvae, pupae) for each colony. Additionally, we carried out sampling using mini-Winkler extractors (Fisher 1998). For the Winkler sampling, ethanol receptacles at the bottom of extractors were replaced by plastic cups containing a humid sponge, for the ants to be collected alive (Silva and Brandão 2014) enabling additional observations.

Species identification of *M. ayri* (Fig. 3) was performed through comparison with the holotype deposited in the Museu de Zoologia da Universidade de São Paulo (MZSP). *Mycetophylax faunulus* (Wheeler 1925) (Fig. 4a, b) was identified by comparison with the material deposited in the Coleção Entomológica do Museu Paraense Emílio Goeldi (MPEG) and an unidentified species of the *Apterostigma* genus, belonging to the Auriculatum species group (Fig. 4c, d) was identified according to the delimitation of species groups provided by Lattke (1997). An expert (Dr. Joice Paulo Constantini, MZSP) performed the termite species *Nasutitermes guayane* (Holmgren 1910) identification. The specimens were deposited in the collections of the MPEG and MZSP. We obtained high-resolution images using a Leica M205C magnifying stereoscope attached to a Leica DFC 425, at the MPEG.

Results

Five colonies of *M. ayri* (Table 1) were found, four epigeic (near the soil surface within the leaf litter) and a single hypogeic colony (below ground). The number of adult individuals in five colonies of *M. ayri* ranged from 27 to 176. The number of alate queens present in these colonies ranged from two to five, and no males were found. When a colony was disturbed, the workers did not show aggressive behavior or appear to defend the brood (Fig. 5).

The first colony (Colony #1, Table 1; Fig. 5) was nesting between two overlapping leaves fallen on the litter on the forest floor. The leaves occupied by the ants were approximately 10 cm long. Among the leaves were queens, workers and immature individuals (larvae and pupae) (Table 1) and some of the workers were arranged in a circle (Fig. 5), holding brood, similar to what Brandão (2003) observed for *M. wallacei* Mann 1916 in Estação Ecológica de Maracá at the Uraricoera River, in the state of Roraima, northern Amazon region, Brazil. The second colony (Colony #2, Table 1; Fig. 2b) was located inside a small twig in the litter, approximately 10 cm in diameter, marked by a highly decomposed degree of decayed wood. There were no other ant species sharing or co-occurring in the twig.

We recorded two colonies (Colony #3 and 4, Table 1; Fig. 2c) within fallen logs in the leaf litter, with a diameter of approximately 150 cm. The two nests were located very close to fungus-farming *Mycetophylax faunulus* ant nests (Fig. 2d). We noticed a worker of *M. ayri* walking on the fungus at the time of collections; however, no interactions between individual workers were observed. In the Colony #4, three workers were observed preying on termites (*N. guayane*).

We recorded a single colony (Colony #5; Table 1; Fig. 2e) in the hypogeic stratum. The nest was not deep (about 5 cm deep), easily located after removing the topsoil at the base of a bush. This nest was very close to the nest of a fungus-farming ant (*Apterostigma* sp.).

When examining the live ants in the mini-Winkler receptacles, we observed two samples with workers and queens of *M. ayri*. As in Colony #1, the ants were arranged in a circle on the humid sponge. We put the ants in Petri dishes in an

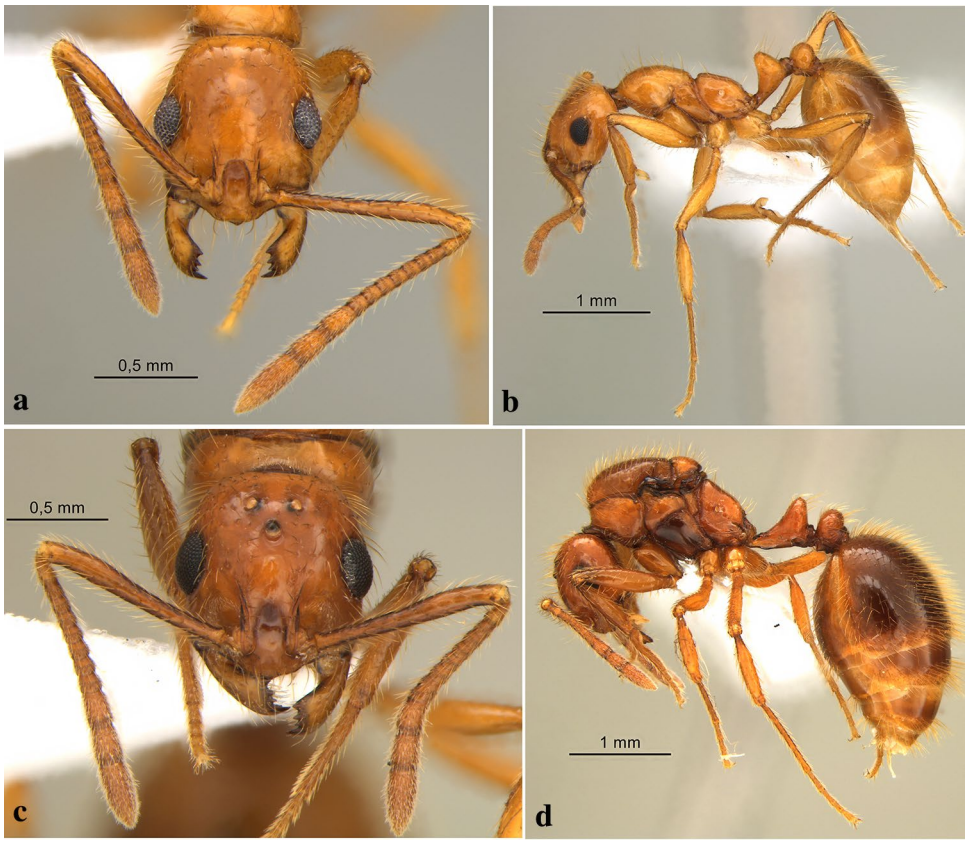

Fig. 3 *Megalomyrmex ayri* (Itaituba, Pará, Brazil). **a** Worker in frontal view; **b** worker in lateral view; **c** queen in frontal view; **d** queen in lateral view

attempt to keep them in laboratory conditions, but in both cases the ants died a several hours later.

Discussion

Since the description of *M. ayri* by Brandão (1990), diversity and ecology studies have reported further records for the species (Guénard et al. 2017). However, the natural history of *M. ayri* remains virtually unknown. Brandão (1990) reported the finding of a polygynous colony by Dr. Ana Harada in the leaf litter, near a small stream in an area of Amazon forest in the state of Rondônia, Brazil (Brandão 1990).

Like most free-living *Megalomyrmex* species, the nest structure of *M. ayri* is not elaborate and lacks detailed substrate manipulation or extensive soil removal. In general, *Megalomyrmex* nests are located in the ground, mainly in the most superficial portion, between the roots of plants or under stones, at the base of trees (e.g., *M. foreli* Emery 1890) or else and more often, they nest in the leaf litter (e.g., *M. brandaoi* Boudinot et al. 2013), occupying fallen twigs or palm leaves (e.g., *M. peetersi* Prado and Adams 2020) and tree trunks (Brandão 1990; Longino 2010; Boudinot et al. 2013). However, colony sizes vary greatly among *Megalomyrmex* species. There are records of the guest ant *M. adamsae* Longino 2010 (Adams et al. 2012) having only a few individuals per colony and of much larger colonies like *M. foreli* (Peeters and Adams 2016) with more than 2000 individuals. Even for *M. goeldii*, which is morphologically similar (Brandão 1990; Brandão 2003) and phylogenetically related to *M. ayri* (Adams 2008), colony size seems to strongly vary. While *M. goeldii* has larger colonies, ranging from 300 (Brandão 1990) to 700 individuals (Morini, unpublished data), *M. ayri* present less than 200 individuals. The number of individuals in a colony can determine the species social organization with strong implications in foraging strategies, colony defense and mating systems, and consequently in the evolution of life histories (Burchill and Moreau 2016).

Megalomyrmex queens are known to vary in number and morphology (winged or wingless) within and among species (Boudinot et al. 2013; Peeters and Adams 2016). As reported by Brandão (1990) and the present study, *M. ayri* colonies are polygynous, with two to five winged queens. The reproductive strategy adopted by a species can influence its dispersion tactics (Molet et al. 2009; Urcuqui et al. 2019).

Megalomyrmex ayri is widely distributed across the Amazon (Brandão 1990; Brandão 2003; Oliveira et al. 2009; Miranda et al. 2012; Santos-Silva et al. 2016; Vicente et al. 2016; Oliveira and Schmidt 2019; Schmidt et al. 2020), and has been recorded also in the Cerrado-Amazon ecotone

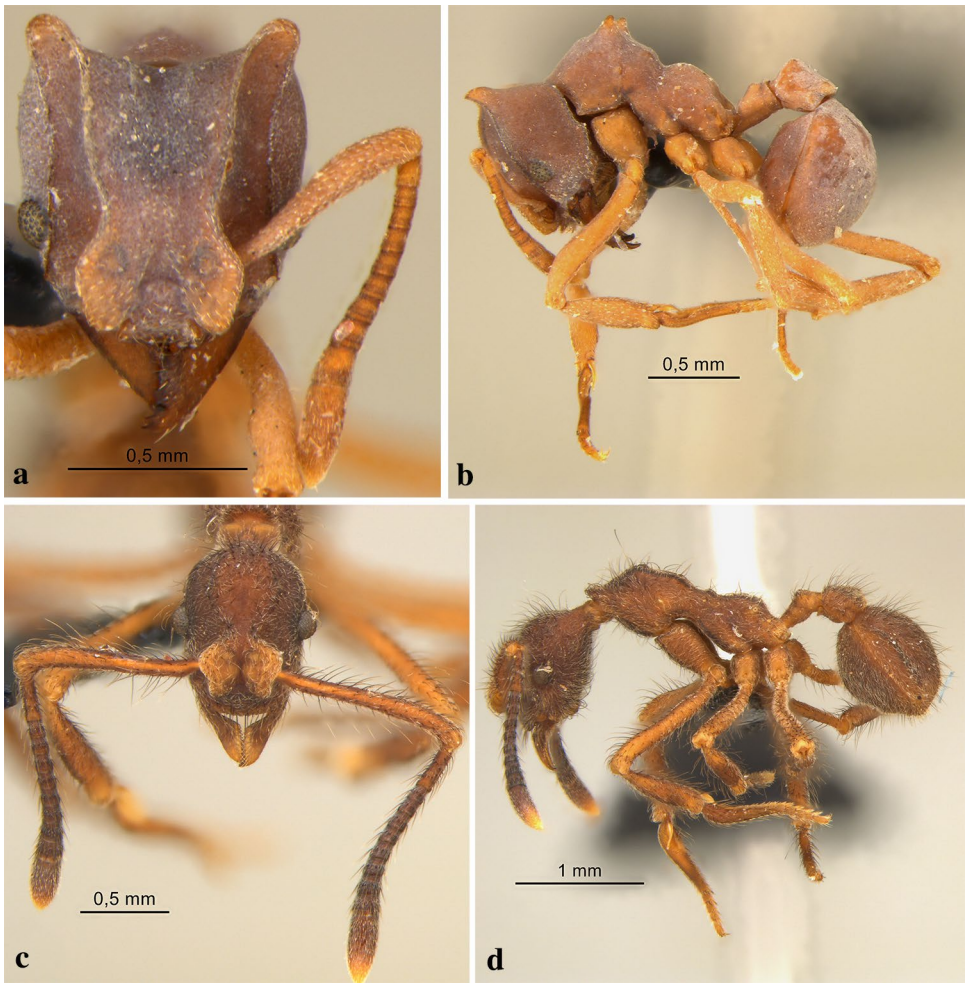

Fig. 4 *Mycetophylax faunulus* (Itaituba, Pará, Brazil). **a** Worker in frontal view; **b** worker in lateral view. *Apterostigma* sp. (Itaituba, Pará, Brazil); **c** worker in frontal view; **d** worker in lateral view

Table 1 Data from the colony of *Megalomyrmex ayri* collected in Itaituba, Pará, Brazil

Colony ID	Eggs	Larvae	Pupae	Workers	Dealate queens	Structure occupied by the colony	Stratum
Colony #1	0	13	14	59	3	Between leaves	Epigeic
Colony #2	0	3	3	49	5	Twig	Epigeic
Colony #3	0	6	9	123	3	Fallen log	Epigeic
Colony #4	11	39	9	171	5	Fallen log	Epigeic
Colony #5	0	18	13	25	2	On the ground	Hypogeic

(Brandão 1990), and in the northern portion of the Atlantic Forest (Brandão 2003; Santos et al. 2017). Incidentally, the present study is the first record of *M. ayri* for the state of Pará. Even if the species is widely distributed so far across two Brazilian biomes, its distribution data show relevant gaps. Although the material available in the literature has not been examined in its entirety, it is possible that specimens identified as *M. goeldii* in Amazon (Baccaro et al. 2010, Miranda et al. 2012, Franken et al. 2013, Souza et al. 2015, Miranda et al. 2017, Fernandes and Souza, 2018, Souza et al. 2018, Torres et al. 2020) are actually *M ayri*. On the other hand, some specimens of *M. ayri* recorded in the Atlantic Forest (Santos et al. 2006, Dias et al. 2008, Dias et al. 2012) can be *M. goeldii*.

Not surprisingly, *M. ayri* appear omnivorous but more work is needed to evaluate their dietary preferences. Individuals were observed preying on *N. guayane* and have successfully been baited with sardines and honey (Santos-Silva et al. 2016) in a forest fragment in the state of Rondônia (Brazil). Despite this probable predatory behavior, when a *M. ayri* colony is disturbed, workers flee without their brood and do not aggressively fight back. The abandonment of their brood is surprising in relation to other ants in general and for *Megalomyrmex* in particular, which until then

Fig. 5 Illustration of the observations made when Colony #1 was found (see Table 1). Queens and part of the workers of *Megalomyrmex ayri* (Itaituba, Pará, Brazil) forming a circle around the brood, while the other workers fled without carrying the immatures

had been reported to keep the larvae between the mandibles when the nest is disturbed. It would be interesting to carry out an experiment to determine whether behaviors related to foraging and colony defense occur through use of chemical weapons and aggressive behavior, as reported by Boudinot et al. (2013) and Sozanski et al. (2020) for *M. peetersi*.

Additionally, three of the five colonies collected were located very close to the nests of fungus-farming species (*Mycetophylax faunulus* and an undetermined species of *Apterostigma*), and in one case, a worker was observed walking inside the *Mycetophylax faunulus* nest. Although interactions between these species have not been actually observed, the nest proximity is intriguing and should be further investigated. There are several *Megalomyrmex* species that are lestobiotic thief ant parasites, consuming fungus garden of different fungus-farming ants (Adams et al. 2015). This lifestyle is, however, restricted to a few species in the Silvestrii group (e.g., *M. silvestrii* Wheeler 1909, *M. mondabora* Brandão 1990, and *M. mondaboroides* Longino 2010) (Adams et al. 2012; Boudinot et al. 2013). Other types of social parasitism (agro-predators and guest ants) have also been found in other *Megalomyrmex* species where garden and host brood are consumed (Adams et al 2000, Adams et al. 2012). The dietary breadth of most *Megalomyrmex* species is, however, currently unknown.

Natural history data remain poorly documented for most ant species (Tschinkel 2003; Diehl-Fleig and Diehl 2007), consequently, the life histories of many species are unknown or only inferred from related species. For *Megalomyrmex,* a few social parasite species have been relatively well studied (Adams et al. 2000; Adams and Longino 2007; Adams et al. 2012, 2013, 2015), but these are of only Central American species. Both social parasitic and free-living *Megalomyrmex* species distributed in the Amazon remain known mostly through ecological surveys. Although distribution maps are currently more complete than before, basic natural history accounts are lacking to piece together the interesting evolutionary history of this genus (but see Cardoso et al. 2016). The use of mini-Winkler extractors that enable ants to remain alive throughout the sampling can also increase or complement natural history data of several species (e.g., Feitosa 2007). Our study expands the knowledge about the natural history of *Megalomyrmex* species, and provides future directions to be explored, such as the presence of chemical defense strategies or symbiotic relationships between *M. ayri* and fungus-farming ants.

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Declarations

Conflict of interest The authors declare no conflict of interest.

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