International Journal of Tropical Insect Science (2026) 46:1733–1741
https://doi.org/10.1007/s42690-026-01812-8

ORIGINAL RESEARCH ARTICLE

Observations on the natural history of the ant-garden, *Azteca paraensis bondari* Borgmeier, 1937 (Formicidae, Dolichoderinae)

Rebeca Q. Menezes[1] · Jacques H. C. Delabie[2,3] · Cléa S. F. Mariano[1] · Elmo Borges de Azevedo Koch[4]

Received: 21 July 2023 / Accepted: 12 February 2026 / Published online: 10 March 2026
© The Author(s) 2026

Abstract

The ant *Azteca paraensis bondari* lives in association with epiphytes in a structure called ant-garden and exhibits trophobiotic interactions with hemipteran species: scale insects (Coccoidea) and other sap-sucking insects. The complexity of these interactions is not fully defined, so this study aims to describe the nesting mode, territorial occupation, and mutualistic interactions around the ant garden system involving *A. paraensis bondari*. Our observations were carried out in a cocoa agroecosystem in the southern region of the state of Bahia, Brazil. Four ant-gardens of *A. paraensis bondari* were observed for 32 h. Each colony presented two types of interactions with hemipteran species and two with epiphytes. The trophobiont scale insect *Coccus viridis* (Coccidae) was common to all observed colonies, as this scale insect uses the epiphyte *Codonanthopsis uleana* (Gesneriaceae) as its food source. The other hemipteran species found associated with the ants are different between the colonies observed. Ants use food resources obtained from epiphyte floral and extrafloral nectaries, in addition to participating in the plant dispersal; they also use honeydew from the scale insects or other Hemiptera they tend. In turn, ants provide nutrients to epiphytes through the organic compost they depose on the ant-garden, actively prey on insects on the host plants and certainly provide dispersion and defense to the scale insects. Our results highlight the remarkable diversity of biotic interactions associated with *A. paraensis bondari*, forming a microcosm known as the "ant garden". This system facilitates nutrient cycling in suspended soils and involves a variety of insects and epiphytes. Additionally, the polydomous structure of the ant colonies contributes to maintain this microcosm in a relative stable equilibrium within the ant's territory. To safeguard *A. paraensis bondari* and its ecological functions, we recommend the establishment of monitoring programs to protect existing colonies and the promotion of agroecological practices that enhace biodiversity within cocoa farms.

Keywords Gesneriaceae · Orchidaceae · Ant-garden · Polydomy · Insect/plant relationships · Neotropical region

✉ Elmo Borges de Azevedo Koch
elmoborges@gmail.com

Rebeca Q. Menezes
rebecaquinto5@gmail.com

[1] Departamento de Ciências Biológicas (DCB), Programa de Pós Graduação em Zoologia (PPGZoo), Universidade Estadual de Santa Cruz (UESC), Laboratório de Artrópodes Sociais, Ilhéus, BA, Brazil

[2] Centro de Pesquisas do Cacau (CEPEC), Laboratório de Mirmecologia, Comissão Executiva do Plano da Lavoura Cacaueira (CEPLAC), Km 22, rodovia Ilhéus-Itabuna (BR-415), Ilhéus, BA, Brazil

[3] Departamento de Ciências Agrárias e Ambientais (DCAA), Universidade Estadual de Santa Cruz (UESC), Ilhéus, BA, Brazil

[4] Departamento de Ciências Biológicas (DCB), Universidade Estadual de Feira de Santana (UEFS), Feira de Santana, BA, Brazil

Introduction

Ant-plant mutualisms are important components in tropical terrestrial environments (Rico-Gray and Oliveira 2008; Orivel and Leroy 2011; da Silva and Santos 2022), such as those well documented between *Azteca* ants and *Cecropia* trees (Urticaceae), *Pseudomyrmex* ants and *Acacia* trees (Fabaceae), and a variety of ants and epiphytes in the Neotropical region. Some of these studies point to convergent evolution between the two groups of organisms, where adaptations that species have developed, favor interactive processes at various levels. These interactions range from intimate interactions, such as the close mutualism that exists between *Azteca* and *Cecropia* (Beattie and Hughes 2008; Oliveira et al. 2015), to facultative and opportunistic interactions, such as protection against herbivory and seed

dispersal (Heil and Mckey 2003; Beattie and Hughes 2008; Heil 2008). Interactions between ants and myrmecophytes bearing extrafloral nectaries are the most commonly studied mutualisms between ants and plants (Dáttilo et al. 2013; Lange et al. 2013; Heil 2015; Del-Claro et al. 2016; Souza et al. 2024).

Ant gardens are certainly among the most advanced cases of interactions between ants and plants (Orivel and Leroy 2011). The expression "ant garden" designates the mutualistic interaction between at least one epiphyte species and one ant species (Belin-Depoux 1991). This remarkable kind of interaction observed exclusively in tropical regions has been relatively neglected in the literature (Vicente et al. 2020). This occurs when arboreal ants actively collect seeds of epiphytes that they cultivate directly on their nests. Such interaction is beneficial for both groups of organisms. The plants provide a protective envelope composed of fibrous and branching roots that spread throughout the nest wall, providing structural integrity to it (Ule 1905; Kleinfeldt 1978). In general, other advantages are added to this, such as the occurrence of extrafloral nectaries on epiphytes, which contribute to the host's feeding (Orivel and Leroy 2011). They also provide a suitable place for the creation of hemipterans associated with these ants by trophobiotic mutualisms, such as *Crematogaster longispina* Emery, 1890 (Kleinfeldt 1978).

On the other hand, epiphytes are favored by the dispersal of their seeds: ant workers are frequently attracted by the fruit pulp itself or by an elaiosome and attractive compounds that surround the seeds (Ule 1905, 1906; Youngsteadt et al. 2010). The ants discriminate the epiphytes with which they are living from other plants thanks to chemical signals (Vicente et al. 2014; Pereira et al. 2021), identifying for example compounds of their seeds (Youngsteadt et al. 2010). They contribute to dispersing them onto a substrate suitable for germination. These seeds are laid in or on the walls of ant nests by the ants (Chautems and Perret 2013; Weissflog et al. 2017).

Azteca paraensis bondari Borgmeier, 1937 is a Dolichoderinae ant that builds "ant gardens" (Ule 1902, 1906; Bondar 1939; Silva 1945; Belin-Depoux 1991; Delabie, 2007). Historically commonly found in cocoa plantations and native forests in the southeastern state of Bahia (Delabie 1990; Delabie et al. 2007), this species maintains numerous biotic interactions with native animals and plants in the Atlantic Forest biome and agroforestry systems of the region. In particular, it forms polydomous colonies where it lives in obligate association with epiphytes of the Gesneriaceae family as well as occasionally with Orchidaceae (Bondar 1939; Silva 1945; Delabie et al. 1991, 2007). Regionally known as "grafting ant", *A. paraensis bondari* is considered harmful to cocoa plantations in southern Bahia, due to physical damages inflicted on the host tree of the "garden" (or phorophyte), as it scrapes the shoots on the upper levels of the tree to extract a gum used to cement the nest (Bondar 1939; Silva 1945; Delabie 1990; Della Lucia 2003).

Intensive campaigns to eradicate this ant were carried out in the cocoa plantations of southeastern Bahia between the 1930s and 1970s (see details in Delabie et al. 2024), which resulted in the near elimination of this species at the regional level. As a consequence, the species is currently not considered to be of economic importance (Oliveira et al. 2015). Although the mutualism *A. paraensis bondari* / Gesneriaceae was cited in revisions about the ant situation in Brazilian cocoa plantations (Delabie 1990; Della Lucia 2003; Delabie et al. 2007), none study focusing this ant-garden was carried out since these campaigns. The aim of this study was to update the information available on the biology of *A. paraensis bondari* in southern Bahia, studying sparse nests in remnant populations and complementing scattered literature data available with new observations. We focus particularly the nesting behavior of the ant and the extreme complexity of the mutualistic interactions between it and a range of organisms.

Materials and methods

Study area

The study was carried out in the municipality of Ilhéus, southern region of the state of Bahia, Brazil (Fig. 1). Observations were made between October 2018 and January 2020, in three experimental areas of the Cocoa Research Center (CEPEC-CEPLAC) (14°45'19" S 39°13'53" W), named "Matinha", "Cacau Velho", and nearby the Extension Center (CENEX).

The vegetation is locally characterized by trees with close or connected canopies. The Matinha and Cacau Velho areas are old experimental cocoa plantations: Matinha is an abandoned cabruca area for over 30 years; and Cacau Velho is a cocoa plantation regionally called "total slash-and-burn" (Cassano et al. 2009). The CENEX area corresponds to the external courtyard of the building where several fruit trees grow.

Sampling design and data collection

The definitions of colony and polydomous nest that we are using are based on Debout et al. (2007) and have been extensively discussed recently about *Azteca chartifex spiriti* Forel, 1912, a phylogenetically close species to the ant under study, which also occurs in the region (Miranda et al. 2021). Nests *sensu stricto* are considered the structures that house

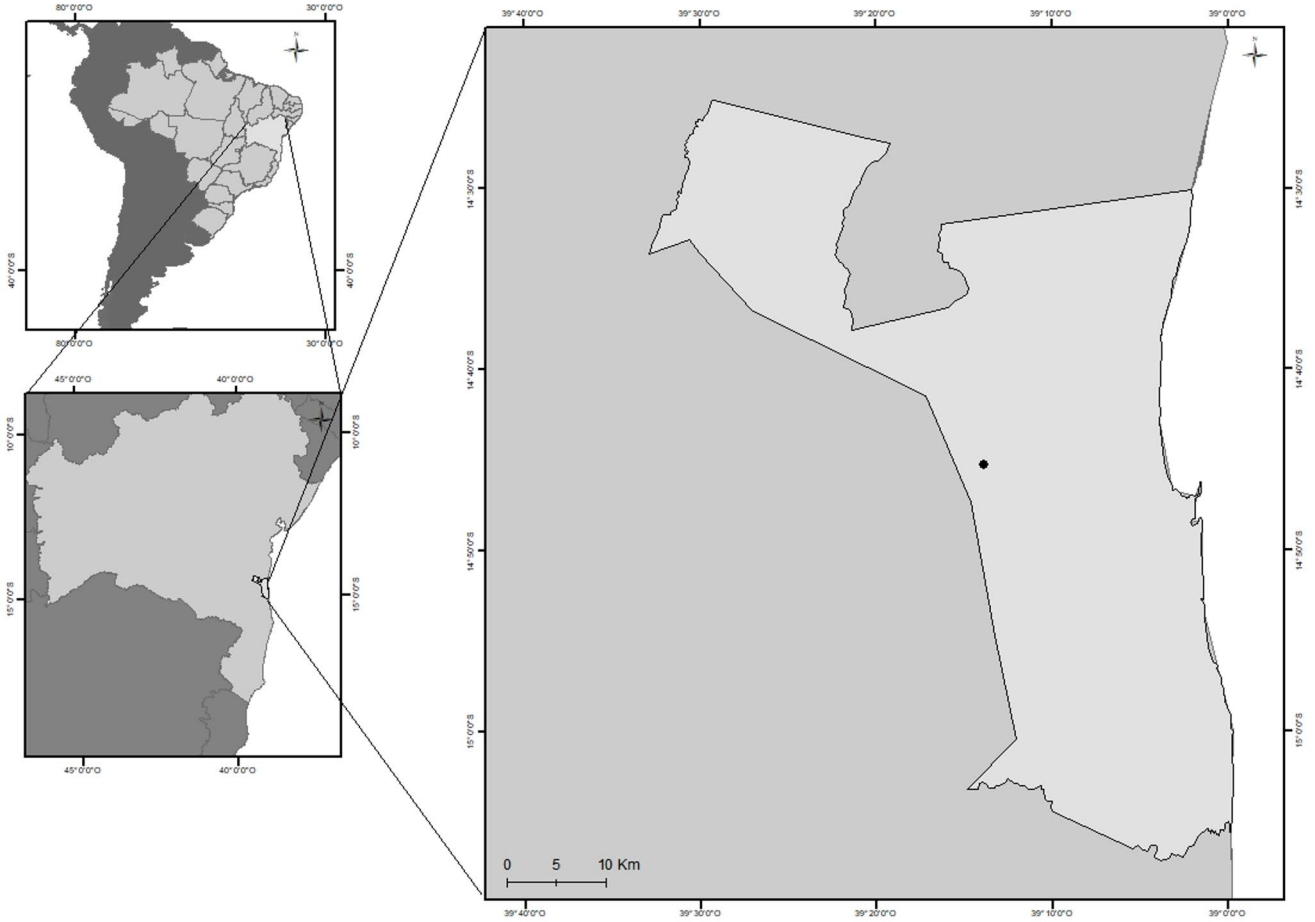


Fig. 1 Map of the region where the study was carried out. The black dot on the larger map represents the location of CEPLAC, located in the municipality of Ilhéus, Bahia, Brazil

ant workers and immatures (eggs, larvae, and/or pupae), regardless of the occurrence of the reproductive female. In turn, satellite structures (shelters for trophobionts) are not considered "true" nests due to the lack of immatures.

We studied three polydomous colonies in the CENEX area and a single one in the Matinha area. Three replications were made per colony, totaling nine observations at CENEX and three at Matinha. The colonies were observed monthly in 2018 (October, November and December) and 2019 (January, February, April and December). As the species is historically of great economic importance in the region, there have been campaigns to control these colonies on cocoa plantations since the 1930s, especially after 1950. Today, regional producers still carry out constant control targeting this species in their farms. Therefore, colonies of this species became quite hard to find, which justifies the low sample number of colonies we observed.

These colonies were selected each one with one main nest (=the largest in the colony considered) and at least two satellite nests, located on the same tree or on two trees with connecting canopies. The activities of the ants within their territory, as well as their interactions with hemipterans and epiphytes, were observed and recorded throughout the observation period. Observations were conducted using a ladder, since the nests were located at heights ranging from two to four meters. Some behaviors were recorded using a camera and a cell phone camera equipped with Cam HD and Full HD capabilities, others were noted on field clipboards. For each colony, the interaction behaviours of the ants with hemipterans and epiphyte species (and any other species that participate in these interactions) were observed. Each colony was studied in the field for a period of four hours per day for two days: two hours in the morning and two hours in the afternoon. Hemipteran species associated with each colony were collected and fixed in 70% alcohol for further identification. The observed nests were collected and carried to the Ant Laboratory of CEPLAC for screening of associated fauna. Samples of epiphytes found in ant gardens were taken to the Geraldo Carlos Pereira Pinto Herbarium (GCPP), of the same institution, for identification. Social wasp nests were photographed for further identification.

Table 1 Location of *A. paraensis bondari* colonies, the host trees in which the colony nests, and the number of Satellite Nests (SN) for each colony. Experimental areas of the Cocoa Research Center, Ilhéus, Bahia, Brazil, October 2018 to January 2020

Colony	Area	Phorophyte	SN
C1	CENEX	*Mangifera indica* L.	4
C2	CENEX	*Spondias purpurea* L.	2
C3	CENEX	*Theobroma cacao* L.	2
C4	Matinha	*Theobroma cacao* L.	2

The identification of associated species was carried out with the assistance of Dr. Jomar Jardim (Federal University of Southern Bahia - UFSB: trees and epiphytes), Dr. Ana Lúcia Peronti (São Paulo State University - UNESP: hemipterans), and Dr. Gilberto Marcos de Mendonça (Federal University of Southern Bahia - UFSB: social wasp nests).

After completing the species identification process, the collected data were organized into a tabular format to analyze the presence or absence of insect and plant species associated with the different colonies of *Azteca paraensis bondari*.

Results

Association of *A. paraensis bondari* with plants in the ant garden

The colonies of *A. paraensis bondari* are polydomous, with an average of three nests per colony, consisting of a main nest and a minimum of 2–5 satellite nests. Within their foraging territory, ants also build shelter structures located at the nodes and internodes of epiphytic branches and host trees. These structures house mutualistic hemipteran species associated with the colonies. The observed nests were built on medium to large trees of different species (Table 1).

Table 2 Epiphytes found in colonies of *A. paraensis bondari* and their spatial location [Main Nest (MN) and Satellite Nest (SN)]. C* - young colony not incorporated into the rest of the study. Experimental areas of the Cocoa Research Center, Ilhéus, Bahia, Brazil, October 2018 to January 2020

Epiphyte species	Ant colony	Location in the ant colony
Codonanthopsis uleana	C1, C2, C3, C4	All nests (NP and NSs)
Coryanthes sp.	C1, C2, C3, C4	NP and NS (larger nests)
Bromeliaceae	C*	NP

The nests have a round and massive shape (Fig. 2), and their structure is formed by vegetal detritus, as well as leaf scraps, insect debris, and certainly ant feces, used as the substrate where the roots of mutualistic epiphytes grow.

During our observations, three species of epiphytes were found living on these nests and participating to the "ant garden": *Codonanthopsis uleana* (Fritsch) Chautems & Mat. Perret (Gesneriaceae); *Coryanthes* sp. (Orchidaceae); in a younger colony, the occurrence of an unidentified Bromeliaceae was also observed (Fig. 2). In turn, the orchid seems to grow on larger and older nests only (Table 2).

The flowering periods of the Gesneriaceae seem to last approximately one month, without a particular seasonality, as we observed open flowers in April, June and October. Open flowers are found together with almost mature or mature fruit. In December some closed flowers were observed too. On the other hand, rarer, orchids were found flowering in October, but in January some closed flowers were seen and in February some fruits were in development.

The roots of *C. uleana* and *Coryanthes* sp. are responsible for supporting the structure and providing rigidity to the ant gardens. At least in the case of *C. uleana*, any new volume added to the ant garden by depositing organic material by workers seems to be quickly seeded (Fig. 3), so that



Fig. 2 Nest of *A. paraensis bondari* (highlighted by the yellow arrow), associated with *Coryanthes* sp. (Orchidaceae) (red arrow) and *Codonanthopsis uleana* (Gesneriaceae) (black arrow)



Fig. 3 Nest of *A. paraensis bondari*, with a recent germinating seedling of *Codonanthopsis uleana* (Gesneriaceae)

the epiphyte seedlings germinate and the roots reinforce the nest substrate cohesion soon.

Associations of *A. paraensis bondari* with floral nectaries and hemipterans

We observed three types of interactions between ants and epiphytes in ant gardens: (a) workers collecting nectar from floral and extrafloral nectaries of at least one of the epiphyte species: in *C. uleana*, floral nectar is collected at the base of the corolla by ants, and extrafloral nectar is collected from small red glands located on the abaxial side of the leaves; (b) workers forage on the plant after fruiting and collect pulp digging small holes in mature and dry fruits of *C. uleana*; (c) ants also explore the cord of the corolla of *Coryanthes* sp. where some of them were observed falling into the opening of the flower without subsequent observation of the worker leaving this compartment.

The observations related to trophobiotic organisms indicate the occurrence of the hemipteran species: scale insects *Coccus viridis* (Green 1889) distributed along the branches, between the gems, on immature fruits and closed flowers, *Saissetia* sp. on the branches at the periphery of the ant territory, and another species close to the genus *Pulvinaria* on leaves and inflorescences (Fig. 4), as well as a species of treehopper (Membracidae) (only immature were observed), all being attended and cared for by workers of ants *A. paraensis bondari* (Table 3). Individuals of the scale insect *Co. viridis* were found only on *C. uleana*, usually on the abaxial region of the leaves, but also on the inflorescences and developing fruits of the same species. The other species of hemipterans were found mainly in shelters built by the ants in the internodes of the leaves of the host trees.

Other elements of the fauna associated with the nests were four species of social wasps (Vespidae), each one nesting near one of the four ant gardens, and established on the same tree that the ant colony: *Angiopolybia pallens* (Lepeletier, 1836), *Parachartergus pseudoapicalis* Willink 1959, *Polybia rejecta* (Fabricius, 1798), and *Protopolybia exigua* (Saussure 1906).

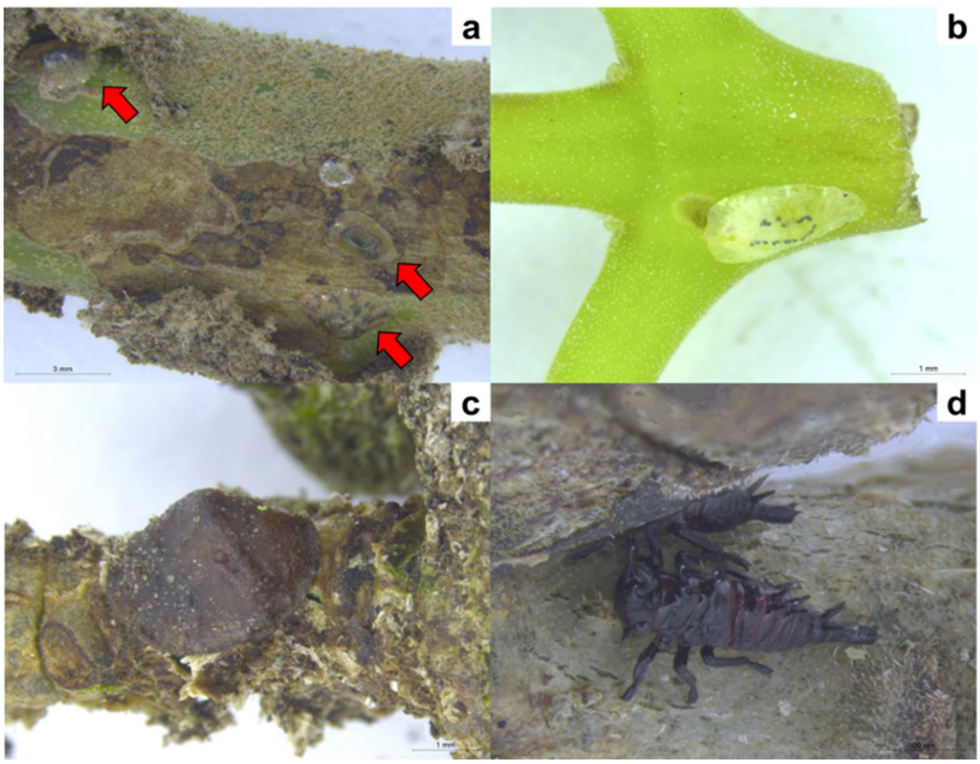


Fig. 4 Hemiptera associated with *A. paraensis bondari*. **A** – Scale-insect species close to the *Pulvinaria* genus (Coccidae), **B** - *Coccus viridis* (Coccidae), **C** - *Saissetia* sp. (Coccidae) and **D** - Unidentified Membracidae

Table 3 Hemiptera observed in trophobiotic relationship with *A. paraensis bondari* and their spatial location within the colonies' territory. Experimental areas of the Cocoa Research Center, Ilhéus, Bahia, Brazil, October 2018 to January 2020

Hemipteran family	Hemipteran species	Colony	Plant family	Plant species	Interaction Place
Coccidae	*Coccus viridis*	C1, C2, C3, C4	Gesneriaceae	*Codonanthopsis uleana*	Branches and shoots
Coccidae	*Saissetia* sp.	C1	Anacardiaceae	*Mangifera indica*	Branches and inflorescence
Coccidae	near *Pulvinaria* sp.	C3	Anacardiaceae	*Theobroma cacao*	Branches and inflorescence
Membracidae	-	C2	Malvaceae	*Spondias purpurea*	Branches and inflorescence

Discussion

Association of *A. paraensis bondari* with plants in the ant garden

Previous observations carried out in cocoa plantations in southern Bahia showed that *A. paraensis bondari* ant gardens were frequently observed on cocoa trees, but also on other trees planted to shade cocoa plantations, such like those of the genera *Erythrina* L., *Genipa* L., *Simira* Aubl., *Inga* Mill., *Trema* Lour., *Sterculia* L. and *Soanea* L. (Bondar 1939; Silva 1945). The ants formed associations with the epiphytes *C. uleana* (=*Codonanthe formicarum*), *Epidendrum flexuosum* G. Mey (=*Epidendrum imatophyllum*), and *Coryanthes maculata* Hook, as well as trophobiotic mutualism with various hemipteran species from the families Aleyrodidae, Aphididae, Coccidae (Bondar 1939; Silva 1945). In the 1950–1970 s, these authors pointed out *A. paraensis bondari* as the worst insect pests of regional cocoa farming, as they held responsible for the weight and size of the ant gardens for breaking the branches of the host tree and damaging its structure as the ants harvest the resin that covers the apical buds causing the entire upper part of the tree to dry out (Delabie 1990).

Polydomy is a term recurrently found in ant literature and designates an arrangement of several independent units of a single society. A range of ant species live in nests with a polydomous structure, as verified with several arboreous ants in the cocoa plantations a Bahia, belonging to the genera *Azteca*, *Camponotus* or *Dolichoderus* (Delabie et al. 1991; Miranda et al. 2021). Different benefits for polydomous colonies are worth mentioning, such as the defense strategy of the ants against predators, easiness access to resources and optimization of use of the tree support (Way 1954; Delabie et al. 1991; Jolivet 1996). *A. paraensis bondari* offers a suitable case of a polydomous ant-garden, having no other equal so sophisticated biological model at the regional level. However, many ant gardens are known from the World's tropical regions (Jolivet 1996; Orivel and Leroy 2011). The benefits of such associations between the epiphytes and the ants are multiple, in particular, if we take into account that the ants may maintain better control of the territory where the nests occur, which is permanently run through by aggressive workers, including the resources found there (sap-sucking Hemiptera for example). The ant population is maintained high there, all nests combined, and the probability of the colony to be eliminated by natural causes is close to zero. On the other hand, the epiphyte population remains high also, subjected to the care of ants who distribute them throughout the habitat on sites favourable to their germination. All this contributes to maintain this microcosm in relative equilibrium within the ant's territory.

Gesneriaceae forms an obligatory mutualism with the ant and is systematically found in all its "ant gardens" observed in the region (Delabie 1990; Delabie et al. 1991). Studies carried out in other regions also showed that Gesneriaceae family and their genera *Codonanthe* and *Codonanthopsis* can be found associated with ants of the genera *Anochetus*, *Azteca*, *Camponotus*, *Crematogaster*, *Dolichoderus*, *Odontomachus* and *Solenopsis* (Wheeler 1921; Weber 1943; Madison 1979; Catling 1997; Quinteros-Gómez et al. 2024). The visit to fruits and removal of seeds by workers (in *C. uleana*) has already been documented for these ant genera, and all of them were observed visiting mature fruits of *Codonanthe* (Madison 1979).

Younger nests of *A. paraensis bondari* with seedlings of *C. uleana* and Bromeliaceae were also observed. Many of these epiphytes depend on association with ants for their growth (Huxley 1980), since soil rich in organic matter favors the growth of this kind of plant (Longino 1986; Blüthgen et al. 2001; Orivel and Leroy 2011). The compost used by the ants to sow the epiphytes, which first serves as the base of the ant nest structure, contributes to the formation of a true suspended soil.

Associations of *A. paraensis bondari* with floral nectaries and hemipterans

In one case, the workers of *A. paraensis bondari* were observed visiting the floral nectaries of *C. uleana* from the anthesis until the beginning of fructification. The interaction with extrafloral nectaries in other ant species was also observed at the beginning of *Codonanthe* anthesis (Madison 1979). These nectaries continue active until the fruit

develops. According to Madison (1979), ants use sometimes their mandibles to perforate the floral corolla, digging a hole that exposes the producing nectar gland. Although we didn't observe this behavior of digging, we saw the ants foraging on floral nectaries through such a hole that we believed that some stingless bees have created to access the floral nectary as some species such as *Trigona* Jurine, 1807, *Bombus* Latreille, 1802 and *Xylocopa* Latreille, 1802 are reputed to have this kind of behavior (Irwin et al. 2010). So, the ants use it secondarily to steal the nectar.

Three colonies of *A. paraensis bondari* studied by us exhibited association with two species of hemipterans, the fourth was found tending only a single species: the scale insect *C. viridis*. This sets them apart from *Azteca sericea-sur* Longino, 2007 (Davidson et al. 2003; Vandermeer and Perfecto 2006; Livingston et al. 2008; Vandermeer et al. 2019) and *Azteca chartifex spiriti* Forel, 1912 (Miranda et al. 2021) which observed only a single species of hemipteran per colony. However, in our study, one of the two species of Hemiptera that develops on *C. uleana* (*Co. viridis*) (Fig. 3) was consistently found in the whole ant gardens.

The spatial distribution of the two distinct groups of trophobionts per ant colony was distinct. This suggests that any competition between the hemipterans is thus avoided (Livingston et al. 2008), but we suggest that the specialization/preference of the sap-sucking insects is according to the host plants available in the environment, frequently different in our observations.

Conclusion

Azteca paraensis bondari exhibits numerous interactions with organisms present in the fauna and epiphytic flora of the canopy. Its nesting model, the "ant garden", influences the survival and dissemination of some native epiphyte and hemipteran species, as well as nutrient cycling in suspended soils. Although the ant population has declined drastically since the 1950s due to severe control measures in cocoa farms, several healthy ant gardens can still be found, particularly in older or abandoned plantations. These nests conserve the same biotic characteristics as those observed by Gregorio Bondar when he first described this mutualism in 1939. Further studies should investigate the importance of this nesting system within the canopy habitat and its relevance to the survival of the organisms associated with it.

To ensure the preservation of *A. paraensis bondari* and its ecological contributions, we recommend the implementation of monitoring programs to protect existing colonies and promote agroecological practices that support biodiversity within cocoa farms. Educational initiatives should raise awareness among local communities and farmers about the ecological and agricultural benefits of ant gardens, emphasizing their role in biodiversity conservation. Additionally, future research should investigate the quantitative contributions of *A. paraensis bondari* to nutrient cycling and epiphyte dispersal, as well as the impacts of modern agricultural practices on this mutualistic system. Integrating *A. paraensis bondari* as a bioindicator in conservation policies and creating ecological corridors with native host trees and epiphytes would further enhance the sustainability of these interactions. This approach not only supports biodiversity but also promotes ecosystem services essential for the health of agroecosystems and broader environmental stability.

Acknowledgements We are grateful to the Programa de Pós-Graduação em Zoologia (PPGZOO) of the Universidade Estadual de Santa Cruz (UESC), the staff of the Laboratório de Artrópodes Sociais (UESC), and Laboratório de Mirmecologia of the Centro de Pesquisa do Cacau (CEPEC/CEPLAC) for logistics. We are grateful to the UESC Herbarium specialist José Lima da Paixão for identifying the trees, Danusa Campos for the map, José Raimundo Maia dos Santos, and Laís S. Bonfim for field support. RQM acknowledges her study grant from FAPESB - BOL0485/2022. JHCD and CSFM acknowledge their research grants form CNPq.

Author contributions RQM: conceptualization, methodology, investigation, writing original draft; JCHD: conceptualization, writing-review & editing; EBAK: writing-review & editing; CSFM: supervision, conceptualization, methodology, writing-review & editing.

Funding The Article Processing Charge (APC) for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614).

Declarations

Conflict of interest The authors have declared there is no conflict of interest.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Beattie AJ, Hughes L (2008) Plant animal interactions: an evolutionary approach. In: Wiley-Blackwell. https://www.google.com/books/edition/Plant_Animal_Interactions/u4jAB7_7srsC?hl=en&gbpv=1&bsq=hughes. Accessed 5 Jan 2023

Belin-Depoux M (1991) Écologie et évolution des jardins de formis en Guyane Française. Rev Ecol 46:1–38. https://doi.org/10.1192/bjp.112.483.211-a

Blüthgen N,Schmit-Neuerburg V, Engwald S, Barthlott W (2001) Ants as epiphyte gardeners: comparing the nutrient quality of ant and termite canopy substrates in a Venezuelan lowland rain forest. J Trop Ecol 17(6):887–894. https://doi.org/10.1017/S0266467401001651

Bondar G (1939) Insetos Nocivos no Cacaueiro. Instituto de Cacau da Bahia, Boletim Técnico no 5, Série Pragas e Moléstias, Bahia, 112

Cassano CR,Schroth G, Faria D, Delabie JH, Bede L (2009) Landscape and farm scale management to enhance biodiversity conservation in the cocoa producing region of southern Bahia, Brazil. Biodivers Conserv 18(3):577–603. https://doi.org/10.1007/s10531-008-9526-x

Catling PM (1997) Influence of aerial *Azteca* nests on the epiphyte community of some Belizean orange orchards. Department Ecol Evolutionary Biology 29:237–242. https://doi.org/10.1111/j.1744-7429.1997.tb00031.x

Chautems A, Perret M (2013) Redefinition of the neotropical genera Codonanthe (Mart.) Hanst. and Codonanthopsis Mansf. (Gesneriaceae). Selbyana 31(2):143–156. https://journals.flvc.org/selbyana/article/view/123019

da Silva EN, Santos RS (2022) Mutualismo, simbiose e protocooperação associada entre formigas, plantas e outros insetos. EDUCTE: Revista Científica do Instituto Fed de Alagoas 13:1943–1956

Davidson DW, Cook SC, Snelling RR, Chua TH (2003) Explaining the abundance of ants in lowland tropical rainforest canopies. Science (1979) 300:969–972. https://doi.org/10.1126/science.1082074

Debout G,Schatz B, Elias M, Mckey D (2007) Polydomy in ants: What we know, what we think we know, and what remains to be done. Biol J Linn Soc 2:319–348. https://doi.org/10.1111/j.1095-8312.2007.00728.x

Delabie JC (1990) The ant problems of cocoa farms in Brazil. Appl Myrmecology World Perspective 1887:555–569

Delabie JHC, Benton FP, de Medeiros MA (1991) La polydomie chez les Formicidae arboricoles dans les cacaoyères du Brésil: optimisation de l'occupation de l'espace ou stratégie défensive. Insectes Soc 7:173–178

Delabie JHC, Jahyny B, do Nascimento IC et al (2007) Contribution of cocoa plantations to the conservation of native ants (Insecta: Hymenoptera: Formicidae) with a special emphasis on the Atlantic Forest fauna of southern Bahia, Brazil. Biodivers Conserv 16:2359–2384. https://doi.org/10.1007/s10531-007-9190-6

Delabie JHC, Santos CD, Santos JT, Santos JL, Bomfim LS, Arnhold A, Koch EBA, Mariano CSF (2024) A formiga caçarema, *Azteca chartifex spirit* Forel, 1919 (Formicidae, Dolichoderinae) na região cacaueira da Bahia, Brasil: ais de um século de amor e ódio. Agrotrópica 36(1,2):35–52.https://doi.org/10.21757/0103-3816.2024v36n1,2P35-52

Del-Claro K, Rico-Gray V, Torezan-Silingardi HM, Alves-Silva E, Fagundes R, Lange D, Dáttilo W, Vilela AA, Aguirre A, Rodriguez-Morales D (2016) Loss and gains in ant–plant interactions mediated by extrafloral nectar: fidelity, cheats, and lies. Insectes Soc 63:207–221

Della Lucia TMC (2003) Hormigas de importancia económica en la región Neotropical. In: Fernández F (ed) Introducción a las hormigas de la región Neotropical. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá 26: 337-351

Della Lucia TMC (2003) Hormigas de importancia económica en la región Neotropical. In: Fernández F (ed) Introducción a las hormigas de la región Neotropical. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, pp 337–349

Dáttilo W, Rico-Gray V, Rodrigues DJ, Izzo TJ (2013) Soil and vegetation features determine the nested pattern of ant-plant networks in a tropical rainforest. Ecol Entomol 38:374–380. https://doi.org/10.1111/een.12029

Heil M (2008) Indirect defence via tritrophic interactions. New Phytol 178:41–61. https://doi.org/10.1111/j.1469-8137.2007.02330.x

Heil M (2015) Extrafloral nectar at the plant-insect interface: A spotlight on chemical ecology, phenotypic plasticity, and food webs. Annu Rev Entomol 60:213–232. https://doi.org/10.1146/annurev-ento-010814-020753

Heil M, Mckey D (2003) Protective ant-plant interactions as model systems in ecological and evolutionary research. Annu Rev Ecol Evol Syst 34:425–453. https://doi.org/10.1146/132410

Huxley C (1980). Symbiosis between ants and epiphytes. Biol Rev 55(3): 321–340

Irwin RE, Bronstein J, Manson JS, Richardson L (2010) Nectar robbing: ecological and evolutionary perspectives. Annu Rev Ecol Evol Syst 41(1):271–292. https://doi.org/10.1146/annurev.ecolsys.110308.120330

Jolivet P (1996) Ants and plants: an example of coevolution (Enlarged edition). Backhuys, Leiden, p 303

Kleinfeldt SE (1978) Ant-gardens: the interaction of *Codonanthe crassifolia* (Gesneriaceae) and *Crematogaster longispina* (Formicidae). Ecology 59:449–456. https://doi.org/10.2307/1936574

Lange D, Dáttilo W, Del-Claro K (2013) Influence of extrafloral nectary phenology on ant-plant mutualistic networks in a Neotropical savanna. Ecol Entomol 38:463–469. https://doi.org/10.1111/een.12036

Livingston GF, White AM, Kratz CJ (2008) Indirect interactions between ant-tended hemipterans, a dominant ant *Azteca instabilis* (Hymenoptera: Formicidae), and shade trees in a tropical agroecosystem. Environ Entomol 37:734–774. https://doi.org/10.1093/ee/37.3.734

Longino JT (1986) Ants provide substrate for epiphytes. Selbyana 9(1):100–103

Madison M (1979) Additional observations on ant-gardens in Amazonas. Selbyana 5:107–115

Miranda VL, Koch E, Delabie JHC et al (2021) Nest spatial structure and population organization in the Neotropical ant *Azteca chartifex spiriti Forel*, 1912 (Hymenoptera: Formicidae: Dolichoderinae). Annales de la Société entomologique de France. (N S) 57(6):499–508. https://doi.org/10.1080/00379271.2021.1994466

Oliveira GV, Corrêa MM, Delabie JHC (2015) Interações planta-inseto: Aspectos biológicos e ecológicos do mutualismo *Cecropia-Azteca*. EntomoBrasilis 8:85–90

Orivel J, Leroy C (2011) The diversity and ecology of ant gardens (Hymenoptera: Formicidae; Spermatophyta: Angiospermae). Myrmecol News 14:73–85

Pereira AA, da Silva IV, Vicente RE (2021) Interaction between epiphytic chemical allelopathy and ant-pruning determining the composition of Amazonian ant-garden epiphytes. Arthropod-Plant Interact 15(3):399–407. https://doi.org/10.1007/s11829-021-09825-5

Quinteros-Gómez Y, Macedo-Bedoya J, Salinas-Inga A, Anlas-Rosado F, Santos-Linares V, Alarcon-Iman G, Gómez-Ticerán D, Angeles-Alvarez F, Olórtegui-Chamolí S, Solis-Sarmiento J, Jara-Peña E, Monroy-Vilchis O (2024) Ant-Plant Mutualism in *Mauritia flexuosa* Palm Peat Swamp Forests: A Study of Host and Epiphyte Diversity in Ant Gardens. Insects 15(12):1011. https://doi.org/10.3390/insects15121011

Rico-GrayV, Oliveira P S (2008). The ecology and evolution of ant-plant interactions. University of Chicago Press. https://doi.org/10.1016/j.biocon.2008.05.021

SILVA, P. (1945). A formiga de enxerto. Instituto de Cacau da Bahia. Boletim de Divulgação, 1:21

Souza LS, Calixto ES, Domingos SS, Bächtold A, Alves-Silva E (2024) Ant protection effectiveness in myrmecophytes and extrafloral nectary plants. J Zool. https://doi.org/10.1111/jzo.13144

Ule E (1902) Ameisengarten im Amazonasgebiet. Botanische Jarbucher fur Systematik 30(2):45–52

Ule E (1905) Wechselbeziehungen zwischen Ameisen und Pflanzen. Flora oder Allgemeine Bot Ztg 94:491–497

Ule E (1906) Ameisenpflanzen Bot Jahrbuch 37:335–352

Vandermeer J, Armbrecht I, De La Mora A, Ennis KK, Fitch G, Gonthier DJ, Hajian-Forooshani Z, Hsieh H-Y, Iverson A, Jackson D, Jha S, Jiménez-Soto E, Lopez-Bautista G, Larsen A, Li K, Liere H, Macdonald A, Marin L, Mathis KA, Monagan I, Morris JR, Ong T, Pardee GL, Rivera-Salinas IS, Vaiyda C, Williams-Guillen K, Yitbarek S, Uno S, Zemenick A, Philpott SM, Perfecto I (2019) The community ecology of herbivore regulation in an agroecosystem: lessons from complex systems. Bioscience 69(12):974–996

Vandermeer J, Perfecto I (2006) A keystone mutualism drives pattern in a power function. Sci (1979) 311:5–9

Vicente RE, Dáttilo W, Izzo TJ (2014) Differential recruitment of *Camponotus femoratus* (Fabricius) ants in response to ant garden herbivory. Neotrop Entomol 43:519–525. https://doi.org/10.1007/s13744-014-0245-6

Vicente RE, Vieira da Silva I, Junqueira Izzo T (2020) Jardins de formigas: qual o estado do conhecimento sobre essas interações mutualísticas entre formigas e plantas? Boletim do Museu Paraense Emílio. Goeldi - Ciências Naturais 15:55–63. https://doi.org/10.46357/bcnaturais.v15i1.236

Way MJ (1954) Studies of the life history and ecology of the *Oecophylla longinoda* Latreille. Bull Entomol Res 45:93–112

Weber NA (1943) Parabiosis in neotropical ant gardens. Ecology 24:400–404. https://doi.org/10.2307/1930541

Weissflog A, Kaufmann E, Maschwitz U (2017) Ant gardens of *Camponotus* (Myrmotarsus) *irritabilis* (Hymenoptera: Formicidae: Formicinae) and *Hoya elliptica* (Apocynaceae). Southeast Asia 9:(e009001):1–16. https://doi.org/10.20362/am.009001

Wheeler WM (1921) A new case of parabiosis and the ant gardens of British Guiana. Ecology 2:89–103

Youngsteadt E, Guerra Bustios P, Schal C (2010) Divergent chemical cues elicit seed collecting by ants in an obligate multi-species mutualism in lowland Amazonia. PLoS ONE 5(12):e15822. https://doi.org/10.1371/journal.pone.0015822

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.