PRELIMINARY EXPERIMENTAL INSIGHTS INTO PARABIOTIC ANT GARDENS AS FUNCTIONAL HUBS IN AMAZONIAN FOREST GAPS

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ABSTRACT: Amazonian Ant Gardens (AGs) are a fascinating mutualism that integrates ants, plants, and epiphytes into complex structural arrangements. Among them, parabiotic AGs, jointly built by *Camponotus femoratus* (Fabricius) and *Crematogaster levior* (Longino), stand out for their wide distribution and role as effective ecosystem engineers. This integrative study investigates how these symbiotic consortia couple fundamental ecological processes, such as biotic defense and decomposition, in southern Amazonian tree-fall gaps. We evaluated the effect of AGs on defense against herbivores in plants with and without extrafloral nectaries (EFNs) and their influence on the colonization of *Cecropia sciadophylla* petioles by invertebrates. The presence of AGs significantly reduced herbivory and enhanced ant defensive responses, but only in EFN-bearing plants. Conversely, petiole colonization was primarily determined by size rather than by the direct presence of AGs, although the composition of the decomposer fauna was notably shifted. These findings demonstrate that parabiotic Ant Gardens play a multifaceted structuring role in Amazonian gaps, influencing different trophic levels and functionally connecting the canopy and soil through a coupled network of ecological interactions.

Keywords: mutualism, *Camponotus femoratus*, *Crematogaster levior*, ecosystem engineering, Amazon rainforest, herbivory, decomposition, tree-fall gaps.

RESULTADOS EXPERIMENTAIS PRELIMINARES SOBRE JARDINS DE FORMIGAS PARABIÓTICAS COMO CENTROS FUNCIONAIS EM CLAREIRAS NA FLORESTA AMAZÔNICA

RESUMO: Os Jardins de Formigas (JFs) amazônicos constituem um mutualismo fascinante que integra formigas, plantas e epífitas em arranjos estruturais complexos. Os JFs parabióticos, construídos conjuntamente por *Camponotus femoratus* (Fabricius) e *Crematogaster levior* (Longino), destacam-se por sua ampla distribuição e por atuarem como efetivos engenheiros de ecossistema. Este estudo integrativo investiga como esses consórcios simbióticos acoplam processos ecológicos fundamentais, como defesa biótica e decomposição, em clareiras de dossel na Amazônia meridional. Avaliamos o efeito dos JFs na defesa contra herbívoros em plantas com e sem nectários extraflorais (EFNs) e sua influência na colonização de pecíolos de *Cecropia sciadophylla* por invertebrados. A presença dos JFs reduziu significativamente a herbivoria e intensificou a resposta defensiva das formigas, mas apenas em plantas com EFNs. Por outro lado, a colonização dos pecíolos foi determinada principalmente pelo tamanho, e não pela presença direta dos JFs, embora a composição da fauna decompositora tenha sido alterada. Nossos resultados demonstram que os JFs parabióticos desempenham um papel estruturante multifacetado nas clareiras amazônicas, influenciando diferentes níveis tróficos e conectando funcionalmente o dossel e o solo por meio de uma rede acoplada de interações ecológicas.

Palavras-chave: mutualismo, *Camponotus femoratus*, *Crematogaster levior*, engenharia de ecossistemas, Amazônia, herbivoria, decomposição, clareiras.

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INTRODUCTION

Amazonian Ant Gardens (AGs) are specialized mutualisms between ants and epiphytic plants, in which seeds of associated epiphytes are planted by ants and germinate in substrates formed by the colonies themselves (Orivel & Leroy, 2011; Vicente et al., 2020). In Neotropical regions, particularly the Amazon, these systems reach remarkable ecological and functional complexity, standing out as hotspots of mutualism (Morales-Linares et al., 2021a, b; Carrias et al., 2012; Céréghino et al., 2010; Leroy et al., 2013). Among the ant species composing AGs, the association between *Camponotus femoratus* (Fabricius, 1804) (Formicinae) and *Crematogaster levior* Longino, 2003 (Myrmicinae) represents one of the most emblematic examples of tropical parabiosis (Vicente & Izzo, 2017; Dacquin et al., 2021). These species share trails, resources, and nests built from plant material and detritus, forming platforms that host typical epiphytes such as *Peperomia macrostachyos* and *Codonanthopsis* spp. (Leal et al., 2017; Vicente et al., 2014; Anjo-Pereira et al., 2021).

Recent studies indicate that such symbiotic consortia exert effects beyond the nest, influencing the structure of surrounding plant and animal communities, both through direct ecological interactions and via indirect pathways mediated by shared partners (Silva-Viana et al., 2021; Vicente & Izzo, 2021; Neundorf et al., 2025). In Amazonian tree-fall gaps, which function as dynamic successional environments, parabiotic ant gardens can increase epiphyte density (Paolucci et al., 2016) and alter patterns of interaction in neighboring plants, modulating pollination and herbivory (Ferreira et al., 2021; Silva-Viana et al., 2021). Although the net cost of ant attendance to pollination tends to be low and context dependent (Vieira da Silva et al., 2025), variation in ant activity around reproductive structures may nonetheless influence selective pressures on traits mediating defense and pollinator attraction in plants bearing extrafloral nectaries. At the community level, the sharing of protective ants among co-occurring plant species can further propagate indirect effects, even when these do not translate into strong differences in herbivory (Souza et al., 2024), reinforcing the idea that these systems operate as interconnected networks rather than isolated pairwise mutualisms. Such cascading effects extend to broader patterns of species diversity (Vicente & Izzo, 2021), highlighting the role of ant gardens as ecosystem engineers sensu Jones et al. (1994), that is, organisms capable of modifying physical and biological conditions to create new microhabitats and influence energy and nutrient flows. In vertically structured Amazonian forests, where gradients of light, humidity, and temperature define ecological niches, these mutualisms operate across multiple dimensions, linking canopy and soil compartments and integrating processes that span distinct forest strata (Vicente et al., 2020; Vicente & Leal, 2025).

This study treats parabiotic Ant Gardens as integrative ecological units and tests whether their presence simultaneously influences (i) biotic defense in plants with and without extrafloral nectaries (EFNs), (ii) spatial dominance and resource monopolization by parabiotic colonies, and (iii) colonization of plant substrates and micro-habitats by decomposer and secondary engineering invertebrates. We hypothesized that (i) AGs enhance ant-mediated defense in EFN-bearing plants, (ii) their behavioral influence extends spatially beyond the nest, modulating community composition and resource use, and (iii) AGs subtly shift decomposer and colonizer assemblages through microclimatic and structural filtering, even if overall colonization rates remain unchanged.

MATERIAL AND METHODS

Study area

The study was conducted in August 2019 during the Field Course of the Graduate Program in Ecology and Biodiversity Conservation (UFMT). Experiments took place in open ombrophilous forest under natural regeneration at Fazenda São Nicolau, Cotriguaçu, Mato Grosso, Brazil (9°51′ S, 58°14′ W – Figure 1). The climate is humid tropical (Aw, Köppen), with mean annual rainfall of 2,300 mm and temperature of 24 °C. The tree-fall gaps (150–600 m²) exhibited variable densities of parabiotic Ant Gardens. Nests of *Ca. femoratus* and *Cr. levior* were readily recognized by their compact structure and associated epiphytes, mainly *Peperomia macrostachyos* (Vahl), *Codonanthopsis uleana* (Fritsch), and *Philodendron* sp. (Vicente et al., 2014).

Figure 1 – Location of the study area in southern Amazonia.

Influence of Ant Gardens on plant defense against herbivores

To test the hypothesis that the presence of parabiotic Ant Gardens increases plant defense against herbivores, two forest clearings were selected within the study area, one containing Ant Gardens (AGs) and another without them, serving as a control. These clearings were comparable in size, vegetation structure, and light incidence, and thus represented two independent treatments. We selected 75 plants in total: 40 in gaps with AGs (20 with extrafloral nectaries, EFNs, and 20 without) and 35 in gaps without AGs (17 with EFNs and 18 without). On each plant, a live termite was placed on the leaf surface to simulate herbivore attack (Figure 2). The time until the first ant arrived was recorded, with 15 minutes as the maximum observation period. Responses were classified as defense present (attack or removal of the termite) or defense absent (no reaction). Data were analyzed using generalized linear models

(GLMs) with binomial distribution, considering the proportion of defensive responses as the response variable and AG presence, EFN presence, and their interaction as predictors.

Figure 2 – Simulated herbivory experiment on plants with and without extrafloral nectaries, in gaps with and without Ant Gardens.

Spatial dominance and behavioral influence of Ant Gardens

To evaluate the spatial extent of parabiotic dominance, we conducted a baiting experiment in tree-fall gaps containing Ant Gardens (AGs) and in adjacent control gaps without AGs. Four 50 m transects were established, each extending 25 m inside and 25 m outside the mapped boundaries of AGs. Along each transect, baits consisting of small pieces of sardine were alternately placed on the ground and vegetation at 5 m intervals. Observations were conducted for 30 minutes, recording (i) the identity of the first ant species to arrive and (ii) whether the bait was subsequently dominated or monopolized by that species.

For each bait, distance from the nearest AG nest and stratum (soil or vegetation) were recorded. The probability of bait encounter and monopolization was analyzed using generalized linear models (GLMs) with binomial error structure, using AG presence and distance as predictors. Separate models were fitted for each parabiotic species (*Camponotus femoratus* and *Crematogaster levior*).

Effect of Ant Gardens on colonization of plant substrates

To investigate whether Ant Gardens indirectly affect colonization of plant substrates by decomposer invertebrates, 100 dry petioles of *Cecropia sciadophylla* were collected, equally distributed among areas with and without AGs. For each sample, petiole length (cm), stratum (soil or vegetation), and presence/absence of invertebrates were recorded. The effects of predictors on colonization probability were tested using GLMs (binomial family) with both continuous and categorical predictors.

Influence of Ant Gardens on colonization of leaf shelters

To evaluate whether Ant Gardens ants affect the colonization of foliar shelters by invertebrates, we incorporated an additional experiment. Two complementary approaches were conducted in forest gaps with and without Ant Gardens. The first consisted of natural sampling, where 30 plants bearing leaf shelters constructed by lepidopteran larvae were selected in each área (Figure 3). For every leaf containing a shelter, a second, expanded (non-rolled) leaf was collected from the same plant as control. The second approach was experimental, consisting of simulated shelters, created by rolling one leaf and securing it with a paper clip, while another intact leaf was clipped as a control. After three days, both leaves were collected. All samples were bagged individually and transported to the laboratory, where arthropods were sorted and morphotyped to assess abundance and richness per treatment. Data were analyzed using generalized linear mixed models (GLMMs), with area (with or without AGs) and treatment (shelter vs. control leaf) as fixed factors and plant identity as a random factor. The models tested the effects of AG presence on (i) the abundance and richness of colonizing arthropods and (ii) the probability of shelter occupation.

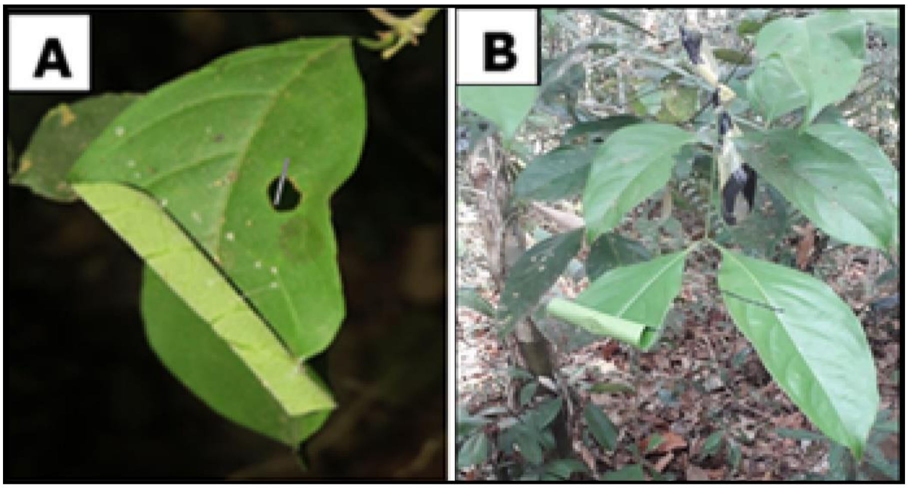

Figure 3 - Natural sampling (A) and simulated leaf shelters (B).

All statistical analyses were performed in R version 4.5.1 (R Core Team, 2025). We used the packages *stats* for GLMs, *vegan* for community analyses (NMDS and PERMANOVA), and *ggplot2* for visualization.

RESULTS

Influence of Ant Gardens on plant defense

Plants in forest gaps with Ant Gardens (AGs) showed higher defensive responses (24 plants) than those without (13 plants). Of the 37 defended plants, 22 had extrafloral nectaries (EFNs) and 15 lacked them (Figure 4). Defensive activity was stronger in EFN-bearing plants across both treatments ($p < 0.05$), but AG presence significantly increased defense frequency and termite removal ($p < 0.01$). In EFN– plants, responses were weaker and independent of AG presence.

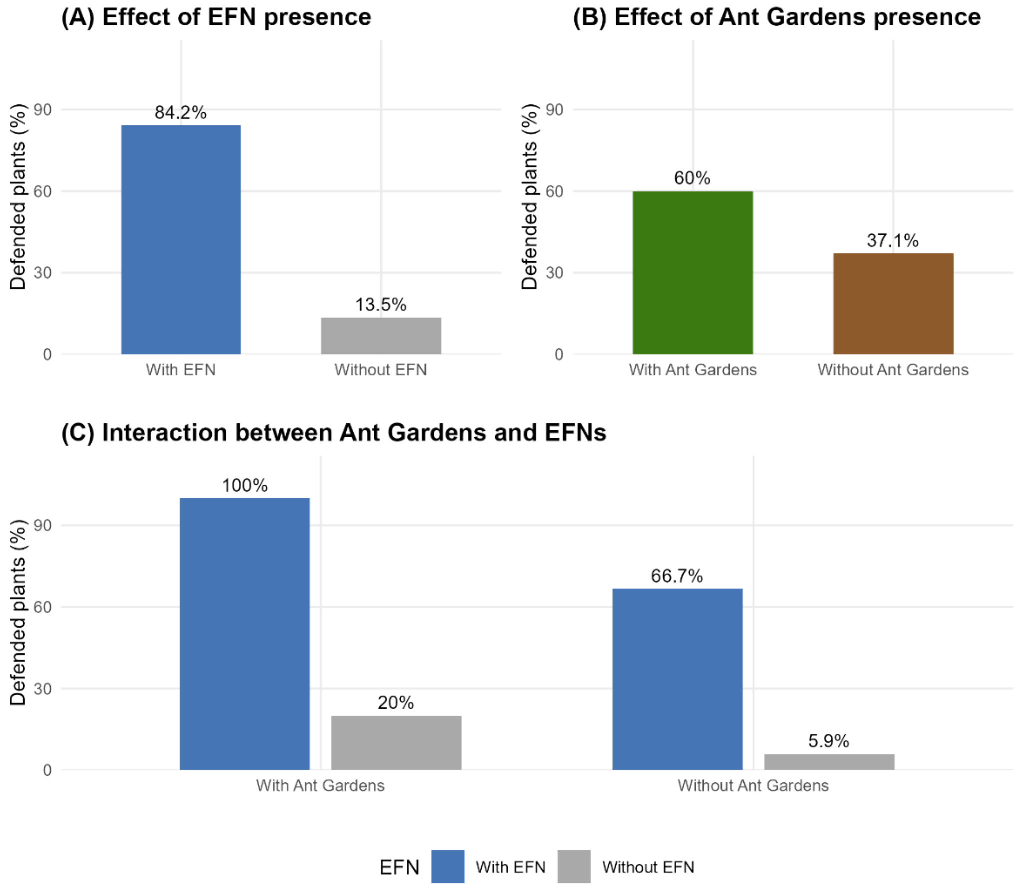

Figure 4 – Defensive responses of plants to simulated herbivory in relation to the presence of extrafloral nectaries (EFNs) and Ant Gardens (AGs). (A) Effect of EFN presence on the proportion of defended plants. (B) Effect of AG presence on defense activity. (C) Interaction between EFNs and AGs, showing that defense frequency was highest in EFN-bearing plants located within AG forest gaps.Values represent the proportion of defended plants (attack or removal of termites) relative to the total number of plants per treatment.

Spatial dominance and behavioral influence of Ant Gardens

Both *Camponotus femoratus* and *Crematogaster levior* exhibited high encounter and dominance frequencies within Ant Garden gaps. The probability of bait encounter decreased gradually with distance from the AG interior (GLM, $p < 0.001$ for both species, Figure 5), but remained above 60% within 15 m.

Ca. femoratus was more efficient in discovering baits, whereas *Cr. levior* dominated them more frequently and extended its dominance slightly beyond the AG limits. Within the garden center, *Cr. levior* monopolized approximately 80% of baits compared to 64% by *Ca. femoratus*; when considered jointly, both species accounted for nearly 100% of bait monopolization.

Stratum (soil vs. vegetation) had no significant effect on encounter or dominance (GLM, $p > 0.05$). In control areas without AGs, bait occupation was lower and more evenly distributed among non-parabiotic species.

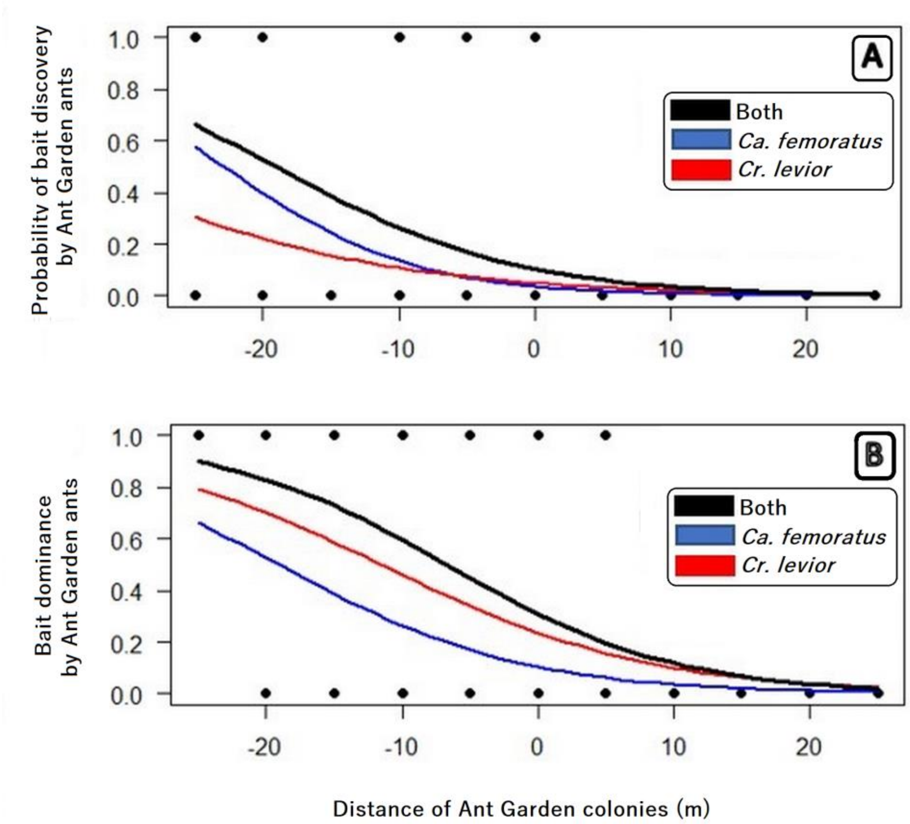

Figure 5 - Proportionality determined between: A) Encounter and B) domination of the Baits by *Crematogaster levior, Camponotus femoratus* and both together in relation to the distance of the Baits from the inside (negative) and outside (positive) of the garden area.

Effect of Ant Gardens on decomposer colonization

Among 100 *Cecropia sciadophylla* petioles, 44% were colonized. Overall occupancy was similar between areas with (48%, Figure 6) and without (40%) AGs, yet differed between strata: in AG areas, occupancy in vegetation (64%) exceeded that on the ground (32%). A similar but weaker pattern occurred in control areas (52% vs. 28%). The ant assemblage colonizing petioles (eight species) responded to AG presence, with slightly higher richness where AGs occurred, seven species (including parabiotic ants) versus six in controls. Other arthropods were mostly found in vegetative strata. Although parabiotic ants did not alter total colonization rates, they modified decomposer composition, promoting more opportunistic ants and fewer non-ant taxa.

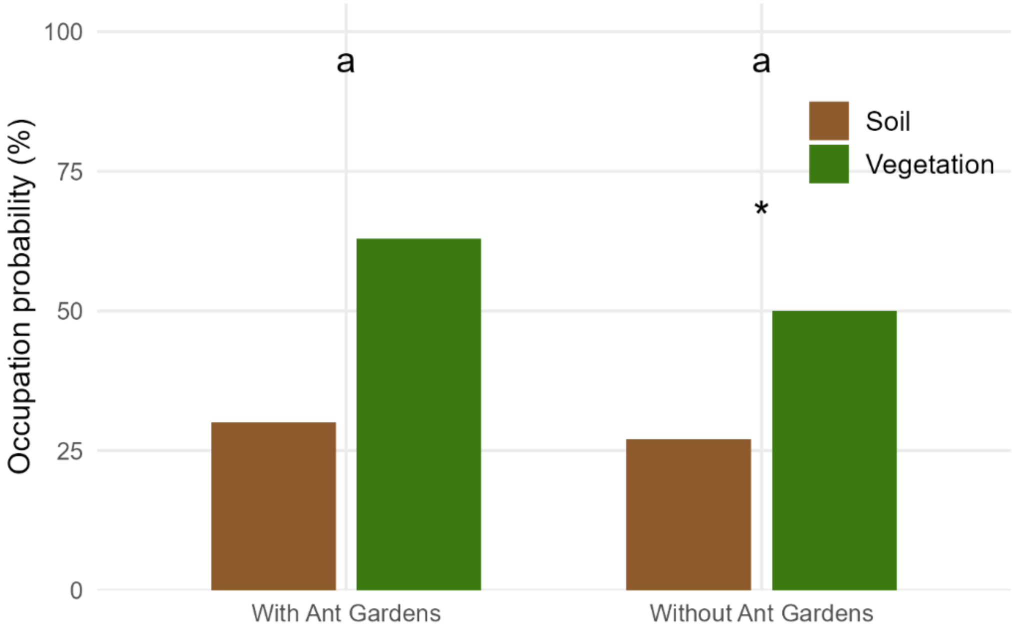

Figure 6 – Probability of invertebrate occupancy of the petiole of *Cecropia sciadophylla* in different strata of forest clearing with and without ant gardens.

Colonization probability was primarily determined by substrate size ($p < 0.01$), regardless of AG presence. Occupancy increases steeply above 60 cm in petiole length, indicating a clear size threshold for colonization (Figure 7a). However, AGs and substrate stratum significantly affected decomposer composition. The distribution of occupied petiole lengths by stratum (Figure 7b), indicate that occupied substrates in vegetation were longer than those on the ground. These results indicate that vertical stratification and substrate size jointly structure decomposer colonization patterns associated with AGs.

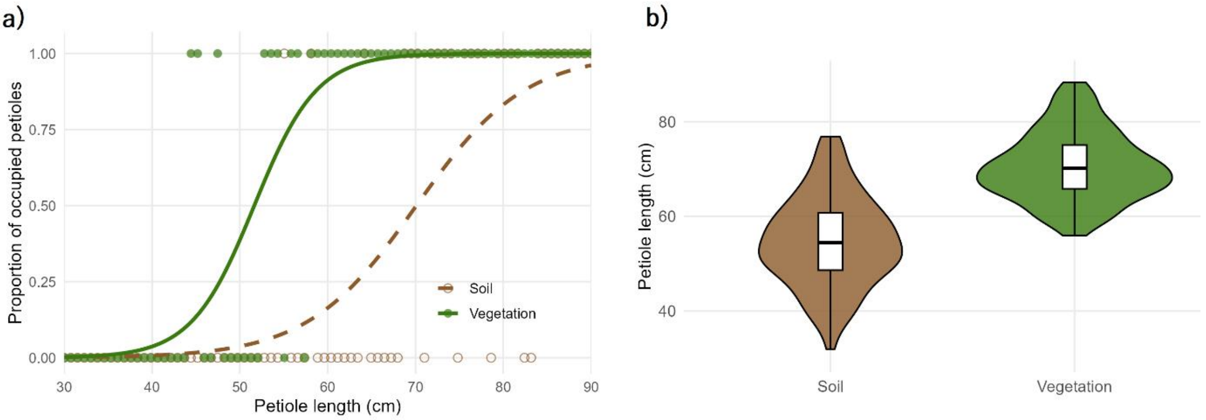

Figure 7 – Colonization patterns of Cecropia sciadophylla petioles by invertebrates. (a) Relationship between petiole length and occupancy probability in soil and vegetation strata. (b) Distribution of occupied petiole lengths by stratum, showing longer occupied substrates in vegetation than on the ground.

Colonization of leaf shelters and micro-habitats

In natural samples, leaves with shelters contained more arthropods than expanded leaves in both areas, but overall abundance was lower within AG gaps. Specifically, outside AG areas, 17 morphotypes were recorded in sheltered leaves and 6 in control leaves, whereas inside AG areas, 9 morphotypes occurred in sheltered leaves and 2 in control leaves.

In experimental trials, where artificial shelters were installed, colonization followed the same trend: outside AG areas, 22 morphotypes were found in shelters and 15 in controls, while within AG areas, only 4 morphotypes were found in shelters and 1 in controls. We have significant effects of treatment and area ($p < 0.001$), confirming higher colonization in leaves with shelters but reduced abundance in the presence of Ant Gardens. The interaction between treatment and area was not significant ($p = 0.88$), indicating that the shelter effect was consistent across both conditions.

The probability of occupation was higher in leaves with shelters located outside AG gaps ($p < 0.001$).

DISCUSSION

Our results reveal that parabiotic Ant Gardens (AGs) act as integrated ecological units that couple behavioral, structural, and microenvironmental processes across Amazonian forest gaps. The enhanced ant activity and reduced herbivory observed in plants bearing extrafloral nectaries (EFNs) near AGs confirm that these colonies extend biotic protection to surrounding vegetation. This diffuse defensive effect aligns with previous field experiments showing that *Camponotus femoratus* and *Crematogaster levior* reduce leaf damage well beyond their nests (Silva-Viana et al., 2021). Similar rapid recruitment responses have been documented both in parabiotic systems and in classical myrmecophytes (Romero & Izzo, 2004; Vantaux et al., 2007; Vicente et al., 2014; Pacheco & Del-Claro, 2018), indicating a convergent behavioral mechanism of defense activation triggered by plant cues. Partner identity and behavioral traits, including worker abundance and aggressiveness, are known to determine the intensity of plant protection in ant-plant systems (Leal et al., 2023; Bruna et al., 2014). These findings collectively support that nectar rewards and ant patrol density interact to maintain an extended defense field encompassing multiple plants and strata.

Bait monopolization patterns reinforce this view; parabiotic colonies dominated resources across the entire 25 m transects, maintaining strong control beyond their nest boundaries and overlapping the area where reduced herbivory was observed. Within AG centers, *Cr. levior* dominated approximately 80% of baits, while *Ca. femoratus* dominated 64%, and together they accounted for nearly full monopolization within the garden area. *Cr. levior* was proportionally more efficient in sustaining dominance farther from the nests, reflecting behavioral asymmetry and complementary division of roles observed in our experiments. Such dominance fields are consistent with the architecture of parabiotic networks, where trails connect the canopy and the forest floor (Vicente & Izzo, 2017). Cooperative parabiosis between *Ca. femoratus* and *Cr. levior* involves a functional division of labor, with *Cr. levior* initiating nest construction while its partner *Ca. femoratus* assumes defensive control as colonies expand, thus ensuring stability across spatial scales (Dacquin et al., 2021). Chemical convergence in cuticular hydrocarbons enhances interspecific tolerance and cohesion (Sprenger et al., 2019), while trophic niche differentiation mitigates competition and stabilizes coexistence. These interactions exemplify behavioral ecosystem engineering (Jones et al., 1994), in which collective behavior produces spatial structuring and habitat modification. Even when dominance does not decrease overall richness, it can reorganize the functional composition of assemblages (Baccaro et al., 2012), consistent with the subtle yet directional shifts observed in our study.

Beyond behavioral control, AG ants modify the physical and biological environment of forest gaps. Differences in decomposer and shelter-dwelling assemblages between AG and control areas indicate that these mutualisms generate distinct microhabitats. Although substrate size remained the main determinant of colonization, AG gaps favored opportunistic ants and reduced termite and beetle abundance, mirroring other systems where dominant ants reconfigure resource use without altering overall richness (Baccaro et al., 2012). Similar processes occur in the epiphytic layer, where pruning and allelopathic filtering by ants structure plant composition and local humidity (Anjo-Pereira et al., 2021; Leal et al., 2017). Accumulated detritus and stable moisture conditions in AGs promote nutrient retention and seedling establishment (Leroy et al., 2013), while microbial and protist communities in associated phytotelmata also shift under ant activity (Carrias et al., 2012). Mutualisms can therefore extend their ecological footprint to entire trophic networks, enhancing functional diversity through cascading effects (Céréghino et al., 2010). These findings position AGs as exemplary cases of organisms that are both ecosystem engineers and providers of ecosystem services, linking habitat modification to ecological regulation (Del Toro et al., 2012; Rocha et al., 2024).

This integrative capacity aligns with the concept of multitrophic conditional mutualisms (Del-Claro, 2016), where ant-plant partnerships influence herbivores, decomposers, and epiphytes simultaneously, and where temporal variation in ant activity can further structure interactions across diel cycles (Córdova Neyra et al., 2026). In AGs, social behavior and structural engineering interact to regulate microclimate, resource flow, and community organization. Habitat structure strongly shapes ant assemblages in Amazonian forests (Olivera et al., 2025), explaining why tree-fall gaps that comprise mosaics of light, temperature, and detrital accumulation, are ideal contexts for such functional coupling (Dáttilo & Izzo, 2012). Abiotic heterogeneity and vegetation structure also underpin the nested organization of Neotropical ant-plant networks (Dáttilo et al., 2013), and disturbance regimes can further reshape interaction architecture and specialization (Souza et al., 2026), supporting the view that parabiotic AGs act as multitrophic nodes connecting behavioral dominance, resource monopolization, and decomposer filtering.

The functional implications of these couplings extend beyond the local scale. Dominant ant species are disproportionately important to the maintenance of ecosystem functions, and their loss under global change may severely impact processes of soil turnover, seed dispersal, and predation (Arnan et al., 2018; Schornobay-Bochenski et al., 2026). At the same time, the robustness of AG networks to environmental disturbance depends on their structural redundancy and mutualistic architecture (Morales-Linares et al., 2021a, b). Functional responses to warming and drought indicate that the persistence of these systems is mediated by both climatic stability and partner complementarity (Dejean et al., 2019, 2022). As Orivel and Leroy (2011) emphasized, AGs epitomize the convergence of social and ecological complexity, combining architectural and behavioral innovation to sustain community resilience. Their widespread distribution across successional habitats further suggests a recurring influence on forest regeneration and microclimatic buffering.

Taken together, these patterns illustrate that parabiotic Ant Gardens are multiscale ecological couplings that integrate defense, competition, and decomposition into a single framework. Their behavioral fields structure the foraging network; their nests and epiphyte matrices regulate the flow of nutrients and energy; and their trophic influence connects canopy and soil across successional stages. Such dual functionality embodies the principle that ecosystem engineering and service provision are complementary sides of the same process (Rocha et al., 2024). By operating at the intersection of behavior, mutualism, and habitat formation, parabiotic AGs exemplify the “little things that run the world” (Del Toro et al., 2012), organisms whose cumulative and recursive actions sustain biodiversity and resilience in the world’s largest tropical forest.

CONCLUSIONS

Parabiotic Ant Gardens constitute remarkable examples of ecosystem engineering in the Amazon rainforest. Their presence reduces herbivory in plants with extrafloral nectaries, enhances living defense, and subtly alters the composition of decomposer communities in plant substrates, favoring opportunistic ant species. These findings demonstrate that Ant Gardens formed by *Camponotus femoratus* and *Crematogaster levior* operate as integrative functional units, capable of coupling ecological processes between the canopy and the forest floor through interconnected mechanisms of habitat engineering, behavioral coupling, and indirect trophic regulation. The action of these ecosystem engineers transcends simple habitat provisioning, actively influencing trophic interactions and community assembly, thus consolidating them as nuclei of mutualism and ecological resilience in the Amazon. Their influence extends across behavioral, structural, and microenvironmental domains, forming multiscale couplings that affect successional dynamics and biodiversity maintenance throughout the Amazon.

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