

Diversity and structure preferences for ant-hemipteran mutualisms in cocoa trees (*Theobroma cacao* L., Sterculiaceae)

Diversidade e preferências estruturais para o mutualismo entre formigas e hemípteros em cacauzeiros (*Theobroma cacao* L., Sterculiaceae)

Elmo B. A. Koch^I  | Thamy E. D. Marques^I  | Cléa S. F. Mariano^{II}  | Esperidião A. S. Neto^{I,II}  |
Alexandre Arnhold^{I,III}  | Ana L. B. G. Peronti^{IV}  | Jacques H. C. Delabie^{I,II} 

^IComissão Executiva do Plano da Lavoura Cacaueira, Ilhéus, Bahia, Brasil

^{II}Universidade Estadual de Santa Cruz, Ilhéus, Bahia, Brasil

^{III}Universidade Federal do Sul da Bahia, Ilhéus, Bahia, Brasil

^{IV}Universidade Estadual Paulista Júlio de Mesquita Filho, Jaboticabal, São Paulo, Brasil

Abstract: The aim of this study is to evaluate the diversity and specificity of ant-hemipteran mutualisms according to the different structures observed on cocoa trees. The experiment was carried out in two cocoa planting systems: *cabruca* and *derruba total* at Ilhéus, Brazil. We made observations and collected monthly over one year the mutualistic ants and hemipterans that occurred on *Theobroma cacao* L. trees. Observations were performed on cacao trees at three distinct sites of the plant: flowers, pods and leaf flush. We observed 932 ant-hemipteran associations, comprising 203 different mutualistic interactions. The assemblage was composed of 26 hemipteran species and 54 ant species. No differences were observed in the ant community, however, we found differences in the hemipteran community according to the different structure evaluated. We recorded a total of 404 trophobiosis events on pods, 394 on leaf flushes and 134 on flowers. Our results point out the diversity of ant-hemipteran trophobioses in the cocoa agrosystems resembles the diversity found in tropical forests and demonstrate that the location of interactions may result in ecological restrictions for some organisms involved in these trophobioses in cacao agrosystems.

Keywords: Formicidae. Hemiptera. Trophobioses. *Theobroma cacao*. Insect-insect relationships.

Resumo: O objetivo deste estudo foi avaliar a diversidade e a especificidade dos mutualismos formigas-hemípteros, de acordo com as diferentes estruturas observadas nas árvores de cacau. O experimento foi realizado em dois sistemas de plantio de cacau: 'cabruca' e 'derruba total', em Ilhéus, Brasil. Fizemos observações e coletamos mensalmente, ao longo de um ano, as formigas e os hemípteros em interações mutualísticas em árvores de *Theobroma cacao* L. As observações foram realizadas em três locais distintos da planta: flores, frutos e lançamentos. Observamos 932 associações entre formigas-hemípteros, compreendendo 203 diferentes interações mutualísticas. Registramos 26 espécies de hemípteros e 54 de formigas. Não observamos diferenças na comunidade de formigas, no entanto, observamos diferença para a comunidade de hemípteros, de acordo com as diferentes estruturas avaliadas. Registramos total de 404 eventos de trofobiose em frutos, 394 em lançamentos e 134 em flores. Nossos resultados apontam que a diversidade de trofobioses nos agrossistemas cacauzeiros se assemelha à diversidade encontrada em florestas tropicais, demonstrando que a localização das interações pode resultar em restrições ecológicas para alguns organismos envolvidos nessas trofobioses nos agrossistemas cacauzeiros estudados.

Palavras-chave: Formicidae. Hemiptera. Trofobioses. *Theobroma cacao*. Relações inseto-inseto.

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Autor para correspondência: Elmo B. A. Koch. Comissão Executiva do Plano da Lavoura Cacaueira. Laboratório de Mirmecologia. Rodovia Ilhéus-Itabuna, km 22. Ilhéus, BA, Brasil. CEP 45600-970 (elmoborges@gmail.com).

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INTRODUCTION

Mutualistic interactions between ants and hemipteran are classified as trophobioses (the relationship in which one species feeds on the other's excretions while provides protection) and are observed in a wide range of host plants and environments, both in natural and agricultural ecosystems (Delabie, 2001; Rico-Gray & Oliveira, 2007). These interactions have been widely studied (Way, 1963; Buckley, 1987; Rico-Gray & Oliveira, 2007; Stadler & Dixon, 2008; Canedo-Júnior *et al.*, 2019; Marques *et al.*, 2018), and most of them are facultative (Rico-Gray & Oliveira, 2007). Ants feed on the excretion of hemipterans, an important sugary resource called honeydew (Way, 1963; Delabie, 2001). This corresponds to the host plant sap metabolized in the digestive tract of the hemipteran partner (Buckley, 1987). The 'honeydew' is a relatively predictable resource and composed of essential nutrients such as amino acids and carbohydrates and, therefore, can sustain high diversity and biomass of arboreal ants (Blüthgen *et al.*, 2000). In contrast, hemipterans are protected from their natural enemies by ants (Way, 1963; Buckley, 1987). In addition, ants remove excess honeydew to prevent fumagine and help hemipterans to disperse on new host plants (Fowler *et al.*, 1991; Delabie *et al.*, 1994). Thus, the ants indirectly contribute to increase the abundance and distribution of hemipterans to get 'honeydew'.

Ant trophobioses usually involve certain costs, such as physiological and developmental constraints, as well as benefits for trophobionts, such as enemy clearance and greater reproductive success (Stadler & Dixon, 2008; Hölldobler & Wilson, 1990). The outcome of different interspecific associations may vary according to the ecological context in which species are involved (Bronstein, 1994; Del-Claro & Oliveira, 2000; Rico-Gray & Oliveira, 2007). Understanding how these conditionality factors – that is, which may influence and thus condition the outcome of mutualistic interactions – has been the goal and challenge of many studies (Cushman & Whitham, 1989; Bronstein, 1994; Chamberlain *et al.*, 2014; Koch *et al.*, 2016).

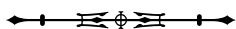
Studies have pointed ant-hemipteran associations to be beneficial to the plant (Eubanks & Styrsky, 2006; Styrsky & Eubanks, 2006). Ants that participate in this type of interactions may be effective for biological control in agricultural systems (Khoo & Ho, 1992; Vandermeer *et al.*, 2002; Eubanks & Styrsky, 2006; Perfecto & Vandermeer, 2006; Jha *et al.*, 2012), since, while defending the source of honeydew, they may reduce the activity of other allegedly harmful herbivores thus contributing for the 'fitness' of the host plants (Vandermeer *et al.*, 2002). In contrast, at high densities, associated ants can also potentiate the deleterious effects of hemipterans such as reducing growth, flowering and fruiting of host plants (Buckley, 1987).

Tropical perennial crops, such as cacao tree (*Theobroma cacao* L., Malvaceae), exemplify agricultural systems in which there is a wide and complex range of interactions between ants and hemipteran (Delabie, 2001; Delabie *et al.*, 2007). As in other ecosystems, the distribution of ants and hemipteran in the cocoa agrosystem may not be random, as ants may associate with hemipteran that produce better quality and larger amounts of honeydew (Bristow, 1991) and hemipterans can be found on specific host plants or parts of them (Cushman & Addicott, 1991). In general, the interactions described can be observed on the stem or the body of flowers and pods, or during cacao leaf flush (Bondar, 1939). The aim of this study was to evaluate the diversity and specificity of ant-hemipteran mutualistic interactions according to the structures of the cocoa trees.

MATERIAL AND METHODS

STUDY AREA

The study was carried out in two different cocoa planting systems (*Theobroma cacao* L., Malvaceae): *cabruca* and *derruba total* (Schroth *et al.*, 2011) at Ilhéus, Brazil. In the *cabruca* system, the forest understory is removed for the implantation of cacao trees, and the planting area is shaded by native Atlantic Forest trees. In this system were



studied three areas, located (one in each) on the farms: São Francisco (14° 45' 04" S; 39° 13' 11" W), Primavera (14° 47' 34" S; 39° 12' 44" W) and Nossa Senhora da Vitória (14° 45' 55" S; 39° 12' 07" W). The distance between the areas was at least two kilometers. In the *derruba total* system, the three studied areas have monospecific shading, generally by species of *Erythrina* sp. (Leguminosae) and the cocoa trees are planted at intervals of three meters. In this system can also be found some fruit trees such as jackfruit (*Artocarpus integrifolia* L. f., Moraceae). The three areas studied in this system are located in the experimental areas of the Cocoa Research Center (CEPLAC) (headquarters: 14° 45' S; 39° 13' W). The distance between the areas was up to 600 meters.

SAMPLING OF ANT-HEMIPTERAN INTERACTIONS

We chose randomly three plots of 50 x 25 m per site, totaling six study areas. The number of trees per plot ranged from 116 to 163. We made observations monthly throughout 2014, and collected the ant and hemipteran species that occurred in mutualistic interactions on all *T. cacao* trees within the plots. Observations in each cacao tree were performed for five minutes on each following structure: flowers, pods and leaf flush, where these interactions are observed more frequently (Figure 1).

SPECIES IDENTIFICATION

The ant specimens were identified in species or morphospecies level by comparison with the reference collection of the Laboratory of Myrmecology at CEPEC/CEPLAC. Hemipteran specimens were identified to species or genus level by experts (Dr. Ana Lúcia Benfatti Gonzalez Peronti and Dr. Olivia Evangelista). However, in many cases, especially when dealing with immatures, specimens of the Membracidae family could not be identified up to species or genus level and were therefore put together into the 'Membracidae group' for data analysis.

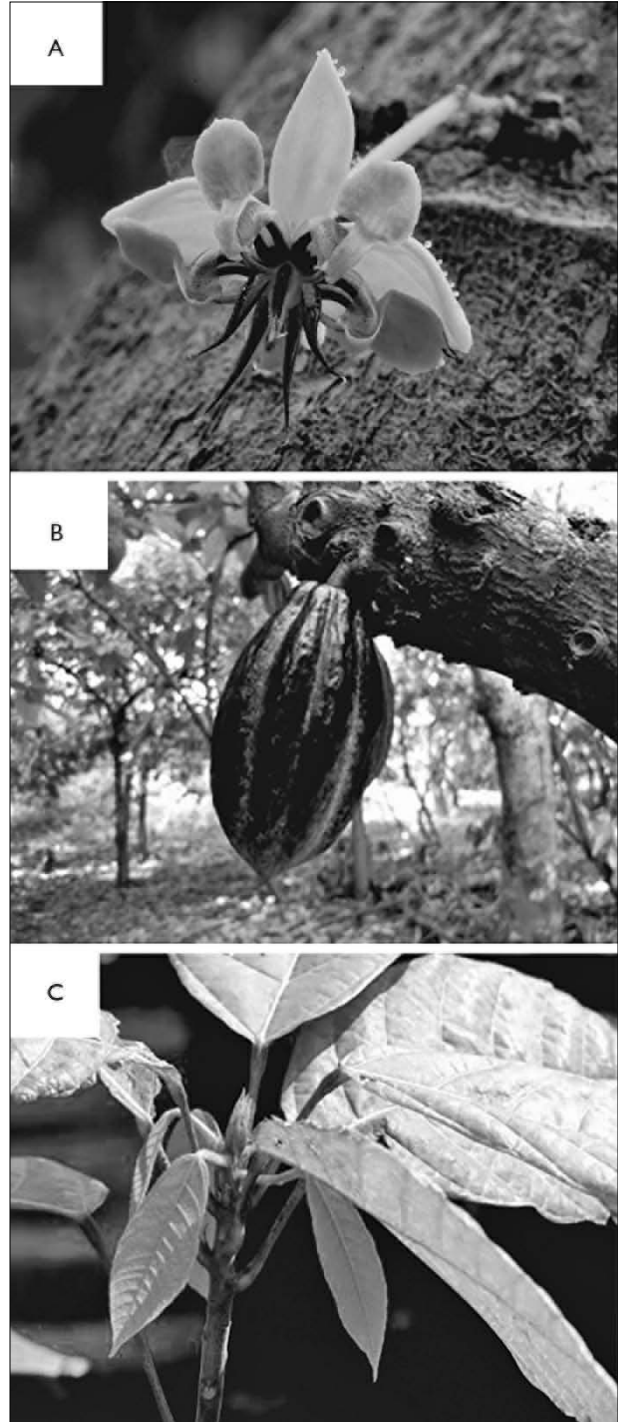


Figure 1. Representative figures of the different structures where mutualistic interactions between ants and hemiptera were observed in *Theobroma cacao* L. (Malvaceae): A) flowers; B) pod; C) leaf flush. Photos: Elmo B. A. Koch (2018).

DATA ANALYSIS

There was no separation of species and interactions between environments for data analysis, since the purpose of the study was to obtain a general overview of interactions and occurrence sites in the agrosystems. To check the number and diversity of interactions between different species as well as the occurrence ratios of interactions as well the local observed in the plant a matrix of the records of the observed interactions was built.

We used the Shannon-Weaner diversity index (H') and Jaccard and Bray-Curtis similarity indexes, respectively, to compare the interactions between hemipteran and ants, regarding diversity and similarity, according to the structure observed on the plant (flower, pod and leaf flush). We used one-way ANOVAs to test the differences in mean values of ant richness, hemipterans richness and trophobioses richness – pairs of interacting species according to the structure observed on the plant (flower, pod and leaf flush), followed by Tukey's post hoc test. To assess the specificity of mutualistic ant-hemipteran interactions according to the structures of the cocoa trees, we performed a Permutational Multivariate Analysis of Variance (PERMANOVA, Anderson, 2001). In this analysis, the frequency of occurrence of each interaction per plot was the response variable, while the predictor variable was the structure of the occurrence (flowers, pods and leaf flush). Statistical significance was obtained by comparisons with a null model (4,999 permutations of the original matrix). All analyzes were performed using R v. 3.5.0 (R Development Core Team, 2018) using vegan 2.3–4 package (Oksanen *et al.*, 2015).

RESULTS

HEMIPTERAN AND ANT SPECIES ASSOCIATED WITH *Theobroma cacao*

We observed 932 mutualistic interaction records of hemipterans and ants on *Theobroma cacao*, comprising 203 different types of interactions. The hemipteran assemblage

interacting with ants was composed of 26 species belonging to four families (Aphididae, Coccidae, Membracidae and Pseudococcidae). In turn, the ants belonged to 54 species in 16 genera and six subfamilies (Appendix). The commonest interactions in the whole study were between the hemipterans *Horiola picta* (Coquebert, 1801), *Anobilia* sp.1, *Planococcus minor* (Maskell, 1897) and *Toxoptera aurantii* (Boyer de Fonscolombe, 1841) and the ants *Dolichoderus bispinosus* (Olivier, 1792), *Dolichoderus bidens* (Linnaeus, 1758), *Azteca charifex spiriti* Forel, 1912, *Solenopsis geminata* (Fabricius, 1804), *Ectatomma tuberculatum* (Olivier, 1792) and *Wasmannia auropunctata* (Roger, 1863) (Appendix).

We found a total of 12 species of hemipterans on flowers, 24 on pods and 23 on leaf flush. The Membracidae *Neotynelia nigra* (Funkhouser, 1940) was found exclusively on leaf flush, while *Fulgoromorpha* sp. and *Nipaecoccus* sp. (Membracidae) occurred only on pods. None hemipteran was exclusive to the flowers (Appendix).

We found a total of 28 ant species on flowers, 34 on pods and 45 on leaf flush. We recorded three species occurring exclusively on the flower: *Camponotus textor* Forel, 1899, *Nylanderia fulva* (Mayr, 1862) and *Nylanderia* sp.2; four on pods: *Azteca paraensis bondari* Forel, 1904, *Crematogaster* sp.3, *Pheidole* sp.1 (group Fallax) and *Tetramorium simillimum* Smith, 1851. Among the whole 54 ant species observed, 15 (27.8%) occurred exclusively on leaf flush (Appendix). Among these stands out the most species of the genus *Pheidole* ($n = 5$), in addition to a single species of *Brachymyrmex* – *Brachymyrmex admotus* Mayr, 1887 – and *Pseudomyrmex* – *Pseudomyrmex gracilis* (Fabricius, 1804).

We found, on average, a greater ant richness on leaf flushes (mean \pm SD: 13.33 ± 4.22), followed by pods (12 ± 3.41) and flowers (9.33 ± 4.18). However, these differences were not statistically significant ($F_{2,15} = 1.591$; $P = 0.237$; Figure 2A). Regarding the number of hemipterans, we found a significant difference according to the structure observed on the tree ($F_{2,15} = 13.47$; $P < 0.001$; Figure 2B). We found, on average, fewer

hemipterans on the flowers (4.67 ± 2.07), which was significantly different (< 0.05) from the number of hemipterans found on pods (mean \pm SD: 11 ± 2.97) and leaf flush (10.5 ± 1.87) (Figure 2B). No differences were observed in the ant community composition according to the observation places on the plant (Jaccard: $F_{2,15} = 0.854$; $P = 0.7244$; Bray-Curtis: $F_{2,15} = 0.855$; $P = 0.635$; Figure 3A). However, we found differences in the hemipteran community (Jaccard: $F_{2,15} = 3.965$; $P < 0.001$; Bray-Curtis: $F_{2,15} = 6.179$; $P < 0.001$; Figure 3B). According to the Tukey's honestly significant difference (HSD) test of multiple comparisons, each structure presents an assemblage of hemipterans significantly different from the other ($P < 0.005$).

ANT-HEMIPTERAN INTERACTIONS ACCORDING TO THE STRUCTURES OF THE COCOA TREES

We recorded a total of 404 trophobiotic interactions on pods, 394 on leaf flushes and 134 on flowers. We found significant differences in the number of trophobioses according to the structure of the tree ($F_{2,15} = 6.473$; $P = 0.009$; Figure 2B). The number of interactions observed on flowers (mean \pm SD: 22.3 ± 10.1) was significantly less (< 0.05) than the number of interactions on pods (67.3 ± 18.1) and leaf flushes (66.2 ± 37.4) (Figure 4A). We did find a significant difference in the ant-hemipteran pairs in interaction according to the structure observed on the tree ($F_{2,15} = 10.36$; $P = 0.0014$; Figure 4B). The value observed on flowers (mean \pm SD: 13.3 ± 6.12), was significantly different (< 0.05) than on other structures (leaf flushes = 27.66 ± 7.11 ; pods = 29.3 ± 6.8) (Figure 3B). The diversity of interactions was higher on pods ($H' = 4.30$), followed by leaf flushes ($H' = 4.23$) and flowers ($H' = 3.65$). We found no difference in the composition of interactions (different pairs in interaction) according to the different structures observed on the cocoa trees (Jaccard: $F_{2,15} = 1.056$; $P = 0.304$; Bray-Curtis: $F_{2,15} = 1.148$; $P = 0.224$).

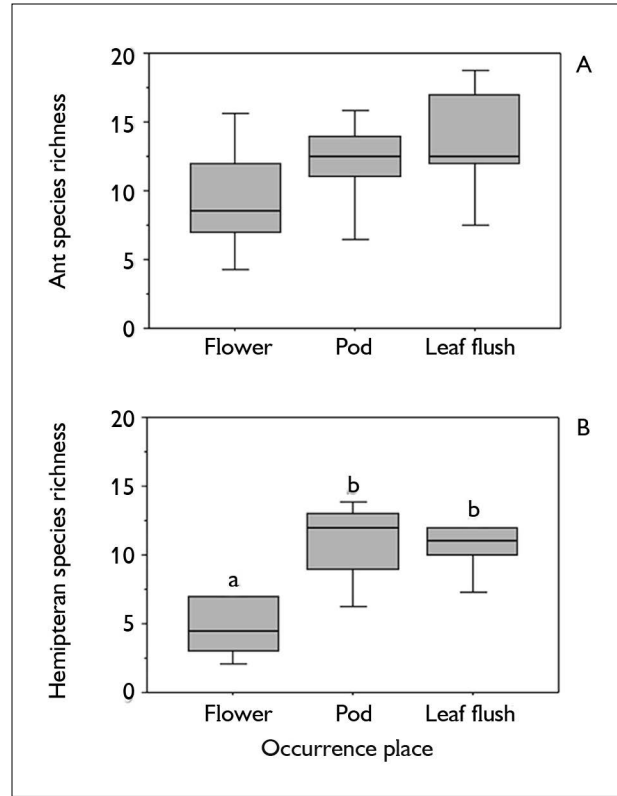


Figure 2. Specific richness of ants (A) and hemipteran (B) according to structure observed (occurrence place) in *Theobroma cacao* L. (Malvaceae). Different letter indicates significant differences between the means.

We observed 57 unique interactions on leaf flushes and 58 on *T. cacao* pods. No interaction was observed occurring exclusively on the flowers. The interactions that were most frequently recorded on flowers were between the hemipteran *Toxoptera aurantii* and the ants *Linepithema neotropicum* Wild, 2007 ($n = 10$), *Dolichoderus bispinosus* (9), *Dolichoderus bidens* (8), *Crematogaster acuta* (Fabricius, 1804) (8), *Azteca chartifex spiriti* (7) and *Solenopsis geminata* (7). Among the most frequent interactions throughout the study, this observation site stands out *Planococcus minor* and *Tropidoscyta* sp.2 that were found interacting, respectively, with a single or two species of ants on the flowers (Table 1).

On the pods, the commonest interactions were between the hemipteran *Anobilia* sp.1 and the ants

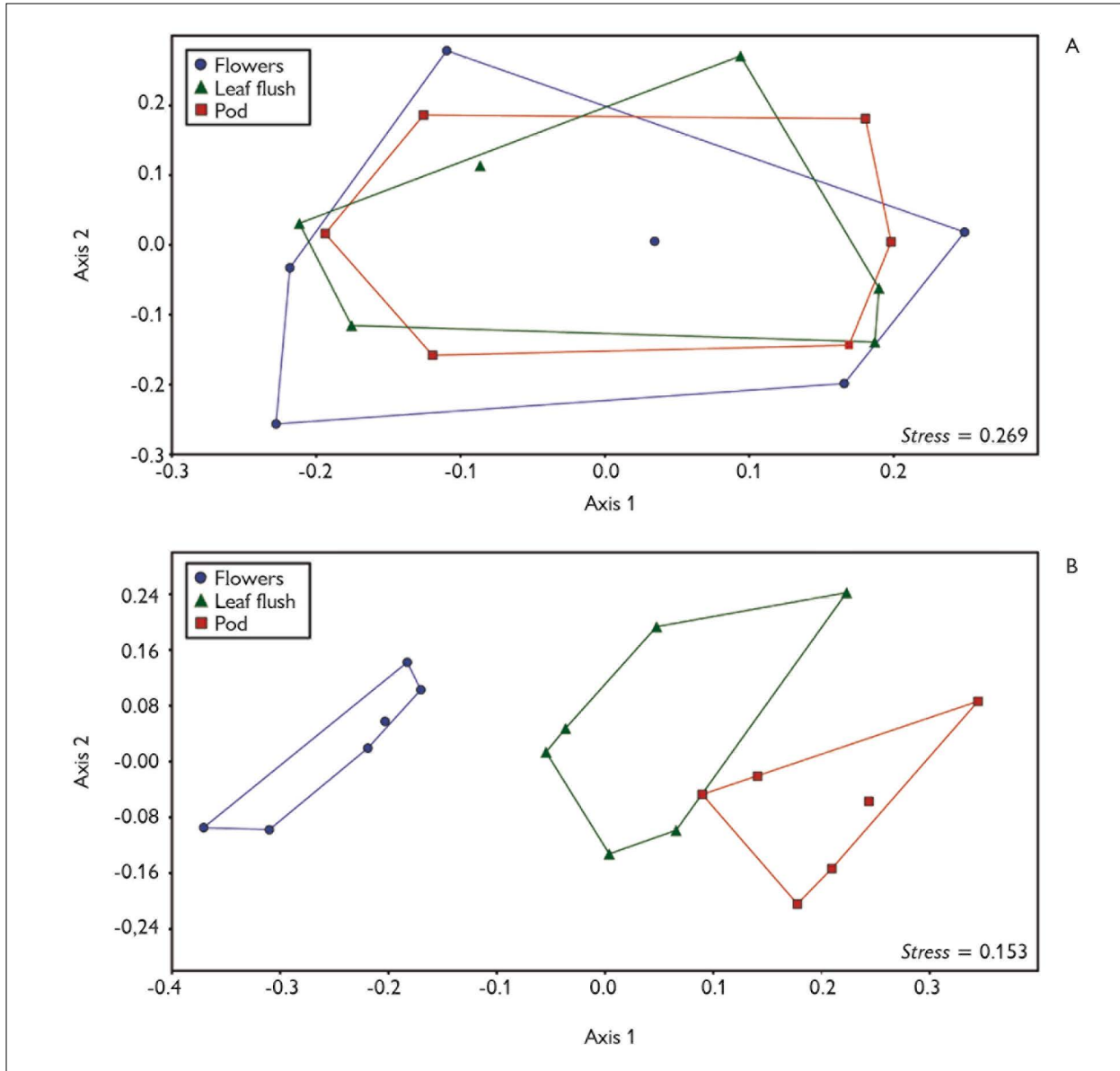


Figure 3. Non-metric multidimensional scaling (NMDS) of (A) ant and (B) hemiptera assemblages, separated according to different structure observed on cocoa trees.

D. bidens (25) and *A. chartifex spiriti* (18); between *P. minor* and the ants *A. chartifex* (17), *W. auropunctata* (17) and *E. tuberculatum* (13 records); and between *Horiola picta* and the ants *A. chartifex spiriti* (16) and *D. bispinosus* (15). The interactions involving *H. picta* and *C. acuta* (7), just like between *Tragopa* sp.2 and *D. bispinosus* (6), were found

exclusively on pods. Among the most frequent interactions seen throughout the study, *T. aurantii* was recorded interacting with eight of the nine most frequently recorded ant species (except *W. auropunctata*, observed interacting with *P. minor* only). Moreover, stands out in this place of observation, the interactions between *Anobilia* sp.1 and *D. bidens* (Table 1).

Table 1. Ant-hemipteran observed interactions (considering the 20 most frequent interactions throughout the study) according to structure observed: flowers, pod and leaf flush in *Theobroma cacao* L. (Malvaceae).

Flowers in <i>Theobroma cacao</i> L. (Malvaceae)							
<i>Tropidoscyta</i> sp.2	<i>Membracidae</i> sp.	<i>Tragopa auriculata</i>	<i>Horiola picta</i>	<i>Anobilia</i> sp.1	<i>Planococcus minor</i>	<i>Toxoptera aurantii</i>	Figure 1A
-	-	-	-	-	-	7	<i>Solenopsis geminata</i>
-	-	-	-	-	3	5	<i>Ectatomma tuberculatum</i>
-	-	-	-	-	-	9	<i>Dolichoderus bispinosus</i>
-	-	-	-	-	-	8	<i>Crematogaster acuta</i>
-	-	-	-	-	1	7	<i>Azteca chartifex</i>
-	-	-	-	-	-	10	<i>Linepithema neotropicum</i>
1	-	-	-	-	-	8	<i>Dolichoderus bidens</i>
-	-	-	-	-	-	6	<i>Monomorium floricola</i>
-	-	-	-	-	-	3	<i>Wasmannia auropunctata</i>
Pod in <i>Theobroma cacao</i> L. (Malvaceae)							
<i>Tropidoscyta</i> sp.2	<i>Membracidae</i> sp.	<i>Tragopa auriculata</i>	<i>Horiola picta</i>	<i>Anobilia</i> sp.1	<i>Planococcus minor</i>	<i>Toxoptera aurantii</i>	Figure 1B
-	-	-	-	-	12	4	<i>Solenopsis geminata</i>
-	-	-	-	-	13	9	<i>Ectatomma tuberculatum</i>
-	4	2	15	-	-	2	<i>Dolichoderus bispinosus</i>
-	-	-	-	-	-	5	<i>Crematogaster acuta</i>
-	-	-	16	18	17	4	<i>Azteca chartifex</i>
-	-	-	-	-	-	1	<i>Linepithema neotropicum</i>
-	-	-	-	25	-	1	<i>Dolichoderus bidens</i>
-	-	-	-	-	-	1	<i>Monomorium floricola</i>
-	-	-	-	-	17	-	<i>Wasmannia auropunctata</i>
Leaf flush in <i>Theobroma cacao</i> L. (Malvaceae)							
<i>Tropidoscyta</i> sp.2	<i>Membracidae</i> sp.	<i>Tragopa auriculata</i>	<i>Horiola picta</i>	<i>Anobilia</i> sp.1	<i>Planococcus minor</i>	<i>Toxoptera aurantii</i>	Figure 1C
-	-	-	-	-	10	18	<i>Solenopsis geminata</i>
-	-	-	-	-	3	14	<i>Ectatomma tuberculatum</i>
-	15	15	23	-	-	16	<i>Dolichoderus bispinosus</i>
-	-	-	-	-	-	12	<i>Crematogaster acuta</i>
-	-	-	4	14	11	14	<i>Azteca chartifex</i>
-	-	-	-	-	-	11	<i>Linepithema neotropicum</i>
7	-	-	-	12	-	11	<i>Dolichoderus bidens</i>
-	-	-	-	-	-	3	<i>Monomorium floricola</i>
-	-	-	-	-	8	7	<i>Wasmannia auropunctata</i>



On the leaf flushes, we recorded commonly the interactions between *H. picta* and *D. bispinosus* ($n = 23$), *T. aurantii* and the ants *S. geminata* (18) and *D. bispinosus* (17). Other interactions commonly observed were among unidentified hemipterans of the Membracidae family with *D. bispinosus* (30). Interactions involving *T. aurantii* and *Camponotus novogranadensis* Mayr, 1870 (4), as well as between Membracidae and *D. bidens* (5), were found exclusively on leaf flushes (Appendix). Among the commonest interactions, *T. aurantii* stands out at this observation site, interacting with all nine most frequently recorded ant species (Table 1). Noteworthy are also *H. picta* and *T. auriculata*, which were found interacting, 15 and 23 times, respectively with *D. bispinosus* (Table 1).

DISCUSSION

Our results show the wide diversity of ant-hemipteran trophobioses in cocoa agrosystems, rather similar to tropical forests (Blüthgen *et al.*, 2000, 2006). The frequency and variety of interactions observed reflect the high diversity of insects and their weak specialization in this agrosystem, as pointed out by several studies (Delabie *et al.*, 2007; Cassano *et al.*, 2009; DaRocha *et al.*, 2015, 2016; Canedo-Júnior *et al.*, 2019). We found variations in the number of ant species and in the number of hemipteran species and assemblage composition in the different structure observed on cocoa tree. The ecological restrictions involved in these trophobioses for some organisms suggest that the tree location where these interactions occur is a conditionality factor of the success of the ant-hemipteran mutualisms on *T. cacao*.

The ants most frequently found in interaction with hemipterans were *D. bidens*, *Cephalotes atratus* (Linnaeus, 1758), *A. chartifex spiriti*, *E. tuberculatum*, *D. bispinosus* and *W. auropunctata*. These species include arboreal ant fauna (except *E. tuberculatum* and *W. auropunctata*, only partially arboreal) commonly found in cocoa agrosystems (Fowler *et al.*, 1991; Delabie *et al.*, 1994, 2007; Delabie, 2001; Marques *et al.*, 2018). In these agrosystems, as also demonstrated in other environments, most interactions

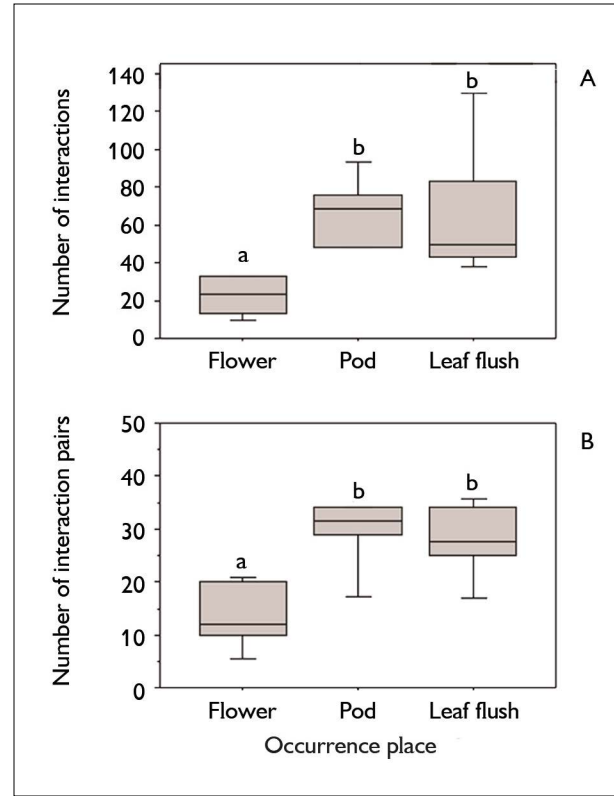


Figure 4. Number of interactions (A) and number of different ant-hemipteran pairs in interaction (B), according to structure observed (occurrence place) in *Theobroma cacao* L. (Malvaceae). Different letter indicates significant differences between the means.

occur through a small number of dominant tree ants, which monopolize most hemipterans (Bigger, 1993; Blüthgen & Fiedler, 2004; Fagundes *et al.*, 2016). Most of these ants contribute to constitute the mosaic of ant dominant ants which are characteristic of the Bahian cocoa plantations (Leston, 1978; Majer *et al.*, 1994).

Most of the ants' associations were with hemipterans of the family Membracidae, which is probably related to the wide diversity of species of this group found in cocoa agrosystems as well as with the easiness of immature manipulation by the ants. However, at the specific level *T. aurantii* (Aphididae) and *P. minor* (Pseudococcidae) were the commonest hemipterans found interacting with ants. The preference of dominant ants for certain species of hemipteran may be related to the quality of honeydew, since there is

variation between species (Blüthgen & Fiedler, 2004). Hemipteran species belonging to the Coccoidea superfamily (e.g. Pseudococcidae) and Aphididae, for example, excrete a nitrogen-rich honeydew (Blüthgen *et al.*, 2003). A second possibility of this preference may be due to the especially high capacity of growth of the population of certain hemipterans (see Delabie *et al.*, 1994 on *P. minor* [then called *Planococcus citri* Risso, 1813] interacting with *W. auropunctata*).

Although ant composition did not significantly vary among the different structures of the cocoa trees, we found significant differences in hemipterans composition. Such result may be correlated with the fact that these organisms have reduced mobility, related to the diversity of feeding strategies they present and dependence on the plants on which they occur. Hemiptera may be highly specialized for specific parts of their host plants (Bernays & Chapman, 1994). The host plant probably affects the composition, abundance and palatability of honeydew of the Hemiptera (Bristow, 1991) and therefore can contribute to motivate the visiting ant. The honeydew is an important resource to the ants (Delabie, 2001; Blüthgen *et al.*, 2000), which are opportunistic when choosing hemipteran to interact (Blüthgen *et al.*, 2006), but their choices may depend on the quantity and quality of honeydew (Cushman & Addicott, 1991). The composition of this resource comprises a wide variety of carbohydrates, lipids and amino acids. Some species of aphids, for example, may produce a higher rate of amino acids in their honeydew than others (Maltais & Auclair, 1952).

Part of the observed interactions was highly related to the structure observed on cacao trees. We found differences in interactions of hemipterans mainly on flowers, when compared with other sites on the tree. No species of hemipteran was exclusive to the flowers, while some interactions were restricted to pods and leaf flushes. Although some species of hemipteran are often found interacting at any of the three different observation sites evaluated, the identity of the partner ant often changes with the place of interaction (Table 1). In fact, studies have

shown that mutualistic interactions are strongly influenced by the environment and the ecological characteristics of where they occur (Cushman & Addicott, 1991; Bronstein, 1994; Chamberlain *et al.*, 2014).

Our results demonstrate that the structure of the tree where the interactions occur is conditioning the ant-hemipteran interactions in cacao agrosystems. However, further studies are needed to determine how our findings could be generalized, as this is the first time that the diversity of trophobiotic hemipterans is explored by considering their interactions with ants according to their location on *T. cacao*. New studies on the management of arboreal insects in cacao trees are necessary too, since certain ant species can effectively control a range of herbivores, especially when associated with certain hemipteran species (Vandermeer *et al.*, 2002; Eubanks & Styrsky, 2006; Perfecto & Vandermeer, 2006; Jha *et al.*, 2012). The location of occurrence (structure on tree) of ant-hemipteran interactions may represent an important conditionality factor of interactions between these insects in cacao agrosystems. A better understanding of these relationships is needed in the context of dependence of the organisms involved in these interactions.

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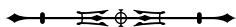


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Appendix. Interactions between ants and hemipterans according to different observation sites in *Theobroma cacao* L. (Malvaceae). (Continue)

Family/Hemipteran species	Ant species	Flower	Pod	Leaf flush	Total
Aphididae					
<i>Toxoptera aurantii</i> (Boyer de Fonscolombe, 1841)	<i>Azteca chartifex spiriti</i> Forel, 1912	7	4	14	25
	<i>Azteca instabilis</i> (Smith, F., 1862)		3	1	4
	<i>Azteca</i> sp.			1	1
	<i>Camponotus</i> (<i>Myrmobrachys</i>) sp.	3		1	4
	<i>Camponotus cingulatus</i> Mayr, 1862	2		2	4
	<i>Camponotus crassus</i> Mayr, 1862	3		3	6
	<i>Camponotus fastigatus</i> Roger, 1863	3	2	1	6
	<i>Camponotus novogranadensis</i> Mayr, 1870			5	5
	<i>Camponotus textor</i> Forel, 1899	1			1
	<i>Camponotus trapezoideus</i> Mayr, 1870			1	1
	<i>Cephalotes atratus</i> (Linnaeus, 1758)	1	2	1	7
	<i>Crematogaster abstinens</i> Forel, 1899			3	3
	<i>Crematogaster curvispinosa</i> Mayr, 1862			1	1
	<i>Crematogaster limata</i> Smith, F., 1858	2	1	1	3
	<i>Crematogaster acuta</i> (Fabricius, 1804)	8	5	12	25
	<i>Crematogaster carinata</i> Mayr, 1862			1	1
	<i>Crematogaster curvispinosa</i>	2	1	3	6
	<i>Crematogaster erecta</i> Mayr, 1866	1	1	3	5
	<i>Crematogaster victima</i> Smith, F., 1858	3			3
	<i>Crematogaster</i> sp.1			1	1
	<i>Crematogaster</i> sp.2			1	1
	<i>Dolichoderus bidens</i> (Linnaeus, 1758)	8	1	11	20
	<i>Dolichoderus bispinosus</i> (Olivier, 1792)	9	2	16	27
	<i>Ectatomma edentatum</i> Roger, 1863	2		1	3
	<i>Ectatomma tuberculatum</i> (Olivier, 1792)	5	9	14	28
	<i>Linepithema leucomelas</i> (Emery, 1894)		1	1	2
	<i>Linepithema neotropicum</i> Wild, 2007	1	1	11	22
	<i>Monomorium floricola</i> (Jerdon, 1851)	6	1	3	10
	<i>Nylanderia fulva</i> (Mayr, 1862)	2			2
	<i>Nylanderia</i> sp.2	1			1
	<i>Odontomachus haematodus</i> (Linnaeus, 1758)		3		3
	<i>Pheidole</i> sp.1	1	2	1	4
<i>Pheidole</i> sp.3	2			2	
<i>Pheidole</i> sp.4			1	1	
<i>Pseudomyrmex gracilis</i> (Fabricius, 1804)			1	1	



Appendix.

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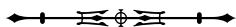
Family/Hemipteran species	Ant species	Flower	Pod	Leaf flush	Total
<i>Toxoptera aurantii</i> (Boyer de Fonscolombe, 1841)	<i>Solenopsis geminate</i> (Fabricius, 1804)	7	4	18	29
	<i>Solenopsis</i> sp.1	1			1
	<i>Solenopsis</i> sp.2			1	1
	<i>Wasmannia auropunctata</i> (Roger, 1863)	3		7	10
	<i>Wasmannia rochai</i> Forel, 1912		1		1
Coccidae					
<i>Coccus</i> sp.	<i>Cephalotes atratus</i>		1		1
	<i>Solenopsis geminata</i> (Fabricius, 1804)			1	1
Membracidae					
<i>Anobilia</i> sp.1	<i>Azteca chartifex spiriti</i>		18	14	32
	<i>Creinatogaster limata</i>		2	2	4
	<i>Creinatogaster acuta</i>	1			1
	<i>Creinatogaster curvispinosa</i>			1	1
	<i>Dolichoderus bidens</i>		25	12	37
	<i>Dolichoderus bispinosus</i>		3	2	5
	<i>Ectatomma tuberculatum</i>	1	8	2	11
	<i>Linepithema neotropicum</i>		2	1	3
	<i>Solenopsis</i> sp.1		1		1
<i>Anobilia</i> sp.2	<i>Cephalotes atratus</i>		7	2	9
	<i>Dolichoderus bidens</i>	2	5		7
	<i>Ectatomma edentatum</i>			1	1
	<i>Ectatomma tuberculatum</i>		1		1
<i>Anobilia</i> sp.3	<i>Azteca instabilis</i>		4	2	6
	<i>Dolichoderus bidens</i>		3		3
	<i>Nylanderia</i> sp.1			1	1
<i>Anobilia</i> sp.4	<i>Azteca chartifex</i> Forel, 1896			1	1
	<i>Dolichoderus bidens</i>		1		1
<i>Aphetea</i> sp.	<i>Azteca chartifex spiriti</i>		2		2
	<i>Cephalotes atratus</i>			1	1
	<i>Dolichoderus bidens</i>		2	5	7
	<i>Dolichoderus lutosus</i> (Smith, F., 1858)		1		1
<i>Bolbonota melaena</i> (German, 1835)	<i>Azteca chartifex spiriti</i>			1	1
	<i>Dolichoderus lutosus</i>			1	1
	<i>Ectatomma tuberculatum</i>		2	1	3
	<i>Solenopsis geminata</i>	1	1		2
	<i>Wasmannia auropunctata</i>	1			1
<i>Bolbonota</i> sp.	<i>Azteca chartifex spiriti</i>		1	3	4



Appendix.

(Continue)

Family/Hemipteran species	Ant species	Flower	Pod	Leaf flush	Total
<i>Bolbonota</i> sp.	<i>Cephalotes atratus</i>			1	1
	<i>Dolichoderus bidens</i>			2	2
	<i>Ectatomma tuberculatum</i>	2	3		5
	<i>Solenopsis geminata</i>		1		1
<i>Fulgoromorpha</i> sp.	<i>Dolichoderus bidens</i>		1		1
<i>Horiola arcuata</i> (Fabricius, 1803)	<i>Dolichoderus attelaboides</i> (Fabricius, 1775)		1		1
	<i>Dolichoderus bispinosus</i>		2	5	7
<i>Horiola picta</i> (Coquebert, 1801)	<i>Azteca chartifex spiriti</i>		16	4	20
	<i>Azteca instabilis</i>		1		1
	<i>Camponotus cingulatus</i>		1		1
	<i>Cephalotes atratus</i>		6	1	7
	<i>Crematogaster abstinens</i>		1	1	2
	<i>Crematogaster acuta</i>		7		7
	<i>Crematogaster curvispinosa</i>	1			1
	<i>Crematogaster victima</i>		1		1
	<i>Dolichoderus bidens</i>		6	4	10
	<i>Dolichoderus bispinosus</i>		15	23	38
	<i>Dolichoderus lutosus</i>		3	1	4
	<i>Ectatomma tuberculatum</i>		7	1	8
	<i>Linepithema neotropicum</i>		1		1
	<i>Monomorium floricola</i>		1		1
	<i>Solenopsis geminata</i>		1		1
	<i>Solenopsis</i> sp.1		1		1
	<i>Wasmannia auropunctata</i>		1		1
<i>Membracidae</i> sp.	<i>Azteca chartifex spiriti</i>	2	8	3	13
	<i>Azteca instabilis</i>		1	2	3
	<i>Camponotus novogranadensis</i>			2	2
	<i>Cephalotes atratus</i>	2	5	1	8
	<i>Crematogaster acuta</i>		1	1	2
	<i>Crematogaster curvispinosa</i>			1	1
	<i>Crematogaster victima</i>		1		1
	<i>Dolichoderus bidens</i>			4	4
	<i>Dolichoderus bispinosus</i>		4	15	19
	<i>Dolichoderus decolatus</i>			1	1
	<i>Dolichoderus lutosus</i>		2		2
	<i>Ectatomma edentatum</i>			1	1
	<i>Ectatomma tuberculatum</i>	4	3	5	12



Appendix.

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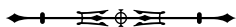
Family/Hemipteran species	Ant species	Flower	Pod	Leaf flush	Total
<i>Membracidae</i> sp.	<i>Monomorium floricola</i>		1	1	2
	<i>Odontomachus haematodus</i>	1			1
	<i>Solenopsis geminata</i>	1		2	3
	<i>Wasmannia auropunctata</i>	1			1
<i>Neotynelia nigra</i> (Funkhouser, 1940)	<i>Cephalotes atratus</i>			1	1
<i>Neotynelia</i> sp.	<i>Cephalotes atratus</i>		1		1
	<i>Dolichoderus bispinosus</i>			1	1
<i>Nipaecoccus</i> sp.	<i>Crematogaster victima</i>		1		1
	<i>Monomorium floricola</i>		1		1
<i>Phormophora</i> sp.1	<i>Cephalotes atratus</i>	2	10	2	14
	<i>Crematogaster curvispinosa</i>		1		1
	<i>Dolichoderus bidens</i>		3		3
	<i>Dolichoderus bispinosus</i>	1			1
	<i>Ectatomma tuberculatum</i>	1			1
<i>Tragopa auriculata</i> (Oliver, 1792)	<i>Azteca instabilis</i>		1		1
	<i>Cephalotes atratus</i>			1	1
	<i>Crematogaster curvispinosa</i>			2	2
	<i>Dolichoderus attelaboides</i>		1		1
	<i>Dolichoderus bidens</i>	1			1
	<i>Dolichoderus bispinosus</i>		2	15	17
	<i>Wasmannia auropunctata</i>			1	1
<i>Tragopa</i> sp.1	<i>Azteca chartifex spiriti</i>		4		4
	<i>Cephalotes atratus</i>		2	2	4
	<i>Crematogaster acuta</i>			1	1
	<i>Crematogaster limata</i>		1		1
	<i>Dolichoderus bispinosus</i>		2	1	3
	<i>Ectatomma tuberculatum</i>			1	1
	<i>Wasmannia auropunctata</i>			1	1
<i>Tragopa</i> sp.2	<i>Azteca chartifex spiriti</i>			1	1
	<i>Crematogaster limata</i>			1	1
	<i>Dolichoderus bidens</i>		5	5	10
	<i>Dolichoderus bispinosus</i>		6		6
	<i>Ectatomma tuberculatum</i>		1		1
	<i>Wasmannia auropunctata</i>			1	1
<i>Tropidoscyta</i> sp.1	<i>Cephalotes atratus</i>		1		1
	<i>Crematogaster acuta</i>		2		2
	<i>Crematogaster curvispinosa</i>		1		1



Appendix.

(Continue)

Family/Hemipteran species	Ant species	Flower	Pod	Leaf flush	Total
<i>Tropidoscyta</i> sp.1	<i>Dolichoderus bidens</i>		1		1
	<i>Ectatomma tuberculatum</i>		2		2
	<i>Linepithema neotropicum</i>			1	1
	<i>Solenopsis geminata</i>			1	1
	<i>Solenopsis</i> sp.2		1		1
	<i>Wasmannia auropunctata</i>			1	1
<i>Tropidoscyta</i> sp.2	<i>Azteca chartifex spiriti</i>		1		1
	<i>Cephalotes atratus</i>		2		2
	<i>Crematogaster acuta</i>			1	1
	<i>Dolichoderus attelaboides</i>		1		1
	<i>Dolichoderus bidens</i>	1	4	7	12
	<i>Dolichoderus bispinosus</i>	1	2		3
	<i>Ectatomma edentatum</i>			1	1
	<i>Ectatomma tuberculatum</i>	2			2
	<i>Linepithema neotropicum</i>			1	1
<i>Tropidoscyta</i> sp.3	<i>Azteca chartifex spiriti</i>		1		1
	<i>Dolichoderus attelaboides</i>			1	1
Pseudococcidae					
<i>Dysmicoccus</i> sp.	<i>Azteca chartifex spiriti</i>		3		3
	<i>Azteca paraensis bondari</i> Forel, 1904		1		1
	<i>Camponotus (Myrmobrachys)</i> sp.1		1		1
	<i>Crematogaster limata</i>			1	1
	<i>Pheidole</i> sp.1		1		1
	<i>Wasmannia auropunctata</i>	1			1
<i>Planococcus minor</i> (Maskell, 1897)	<i>Azteca chartifex spiriti</i>	1	17	11	29
	<i>Azteca instabilis</i>	1	4	1	6
	<i>Brachymyrmex admotus</i> Mayr, 1887			1	1
	<i>Camponotus crassus</i>		1		1
	<i>Cephalotes atratus</i>			1	1
	<i>Crematogaster abstinens</i>		1		1
	<i>Crematogaster curvispinosa</i>	1			1
	<i>Crematogaster abstinens</i>		2		2
	<i>Crematogaster acuta</i>		4	4	8
	<i>Crematogaster carinata</i>			1	1
	<i>Crematogaster curvispinosa</i>			1	1
<i>Crematogaster erecta</i>			1	1	



Appendix.

(Conclusion)

Family/Hemipteran species	Ant species	Flower	Pod	Leaf flush	Total
<i>Planococcus minor</i> (Maskell, 1897)	<i>Crematogaster limata</i>		3	2	5
	<i>Crematogaster</i> sp.2			1	1
	<i>Crematogaster</i> sp.3		2		2
	<i>Crematogaster victima</i>			2	2
	<i>Dolichoderus bidens</i>		3		3
	<i>Dolichoderus bispinosus</i>	1	1	1	3
	<i>Dolichoderus lutosus</i>		2		2
	<i>Ectatomma edentatum</i>			1	1
	<i>Ectatomma tuberculatum</i>	3	13	3	19
	<i>Linepithema neotropicum</i>		3	1	4
	<i>Monomorium floricola</i>		4	4	8
	<i>Nylanderia</i> sp.1	1			1
	<i>Odontomachus haematodus</i>		1		1
	<i>Pheidole ambigua</i> Wilson, 2003			1	1
	<i>Pheidole</i> gr. <i>fallax</i> sp.1		1		1
	<i>Pheidole</i> gr. <i>fallax</i> sp.2		3	1	4
	<i>Pheidole midas</i> Wilson, 2003			1	1
	<i>Pheidole radoszkowskii</i> Mayr, 1884			1	1
	<i>Pheidole</i> sp.2			1	1
	<i>Pheidole</i> sp.3		1		1
	<i>Solenopsis geminata</i>		12	10	22
	<i>Solenopsis</i> sp.1		1	1	2
	<i>Solenopsis</i> sp.2		1	1	2
	<i>Tetramorium simillimum</i> Smith, 1851		1		1
	<i>Wasmannia auropunctata</i>	1	17	8	26
	<i>Wasmannia rochai</i>		2	3	5
	Total		134	404	394



