Diversity of Hemiptera (Arthropoda: Insecta) and Their Natural Enemies on Caryocar brasiliense (Malpighiales: Caryocaraceae) Trees in the Brazilian Cerrado

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Diversity of Hemiptera (Arthropoda: Insecta) and their natural enemies on Caryocar brasiliense (Malpighiales: Caryocaraceae) trees in the Brazilian Cerrado

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Abstract

The Cerrado occupies about 23% of the Brazilian territory and is characterized by great diversity of plants and insects and a great degree of endemism, and Caryocar brasiliense A. St.-Hil. (Malpighiales: Caryocaraceae) is widely distributed in this region. The diversity and abundance of hemipterans and their natural enemies were studied on trees of C. brasiliense in the Cerrado, pasture, and anthropic area in Montes Claros, Minas Gerais State, Brazil. We observed 1 rare, 8 common, and 1 frequent species of sucking insects; and 2 rare, 7 common, and 6 frequent species of natural enemies. Sucking insects and their natural enemies were most abundant in the pasture and least abundant in the Cerrado. Increasing diversity indices and numbers of species and individuals of sucking insects were followed by similar trends in the populations of natural enemies. Increasing populations of sucking insects led to greater numbers of individuals of ants, green lacewings, predator thrips, and ladybeetles. Aluminum level positively affected the number of species and individuals, and the pH of the soil reduced those of sucking insects. Leafhoppers had greater numbers on plants on soils with low pH values and high aluminum levels, but the opposite was noted for the aphids.

Key Words: aphid; leafhopper; mealybug; predator; pequi

Palabras Clave: pulgones; chicharritas; cochinillas; depredadores; pequi

Caryocar brasiliense A. St.-Hil. (Malpighiales: Caryocaraceae) trees have a wide distribution in the Brazilian Cerrado (Brandão & Gavilanes 1992; Bridgewater et al. 2004; Leite et al. 2006a) and can form a canopy of over 10 m height and 6 m width (Leite et al. 2006a, 2011a,b, 2012). The fruits have a mesocarp rich in oil, vitamins, and proteins and contain many compounds of medicinal importance. The tree is also used by humans for food, the production of cosmetics and lubricants, and in the pharmaceutical industry (Araújo 1995; Segall et al. 2005; Ferreira & Junqueira 2007; Garcia et al. 2007; Khouri et al. 2007). This plant is the main source of income in many communities (Leite et al. 2006a).

Caryocar brasiliense trees are protected by Brazilian laws and thus left in deforested areas of the Cerrado. However, in northern Minas Gerais State, in general, their natural regeneration is restricted to areas with impoverished soils (sandy or rocky outcrop) (Leite et al. 2006a). Isolated trees suffer high leaf, flower, and fruit damage from sucking insects (personal communication from collectors of fruits), but this damage is poorly studied (Araújo 1995), mainly due to lack of specialists (Freitas & Oliveira 1996; Oliveira 1997; Lopes et al. 2003; Boiça et al. 2004; Leite et al. 2009, 2011a,b, 2012).

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The diversity and abundance of arthropods can vary among environments, and several hypotheses can explain this fact: 1) complex environments increase the number of herbivore species and their predators associated with a host plant and, generally, decrease their abundance (Auslander et al. 2003; Lazo et al. 2007); 2) host plant attributes such as complex architecture can increase the diversity of herbivorous insects (Espírito-Santo et al. 2007); and 3) soil characteristics that are favorable to trees can indirectly effect herbivorous insects (e.g., through nutritional quality) (Auslander et al. 2003; Espírito-Santo et al. 2007).

We tested, for the first time, these 3 hypotheses—complex environments, host plant attributes, and soil characteristics—in relation to the diversity and abundance of Hemiptera herbivores and their natural enemies on C. brasiliense trees in 3 areas. Each area represented unique habitat conditions: 1) preserved Cerrado, 2) Cerrado cleaned and areas.

## Study Sites

The study was conducted in the municipality of Montes Claros, Minas Gerais State, Brazil, during 3 consecutive years (Jun 2008 through Jun 2011) in 3 areas of a region with dry winters, rainy summers, and Aw climate (tropical savanna) according to Köppen (Vianello & Alves 2000). The areas were: 1) Cerrado sensu stricto (16.7487778°S, 43.9186944°W, at 943 m, with dystrophic red yellow latosol of sandy texture); 2) pasture, formerly Cerrado vegetation (16.7711389°S, 43.9587222°W, at 940 m, with dystrophic red yellow latosol of loamy texture), and 3) anthropic area, campus of the “Instituto de Ciências Agrárias da Universidade Federal de Minas Gerais” (16.6818056°S, 43.8407778°W, at 633 m, with dystrophic red latosol of medium texture) (Leite et al. 2006a, 2011a), near to a vegetable production area (approx. 400 m distance). We used the soil data already published by Leite et al. (2006a, 2011a), who had collected soil samples in the same areas.

The Cerrado sensu stricto (a species-rich dense scrub of shrubs and trees, 8–10 m in height, with a dense understory), common for the Brazilian Cerrado, is an open grassland (Ribeiro & Walter 1998; Durigan et al. 2002). The Cerrado area of our study had 44.87% grass (soil covering), 314.90 ± 20.93 cm³, and areas.

### Study Design

The study was completely randomized with 12 replications (1 tree per replicate) and 3 treatments (areas). Caryocar brasiliense trees were identified in a 600 m straight line per area, and every 50 m a random plant was evaluated. Mature trees of C. brasiliense (producing fruits) were randomly sampled per collection, except in the anthropic area, where trees were evaluated every time.

The number of Hemiptera and arthropod natural enemies was evaluated monthly in the morning on 4 leaves, 4 flowers, and 4 fruits per tree and area by direct observation during 3 yr (Horowitz 1993). Insects on leaves, flowers, and fruits were collected with tweezers, brush, or aspirators and preserved in vials with 70% alcohol for identification.

### Statistical Analyses

The number of sucking insects and natural enemies, species richness, and diversity were calculated per tree and area. All ecological indices were measured by calculating the dataset of taxa by samples in BioDiversity Pro Version 2 software. Hill’s formula (Hill 1973) was used to calculate the diversity and the Simpson indices for abundance and species richness (Lazo et al. 2007). Species of sucking insects and natural enemies were classified as: a) frequent (frequency ≥ 50%), b) common (10% < frequency ≤ 49%), and c) rare (frequency ≤ 10%) in the samples.

Simple regression analyses were made to compare the diversity index, number of individuals, and number of species of sucking insects with the diversity index, number of individuals, and number of species of natural enemies; the numbers of ants, predator thrips and bugs, spiders, ladybeetles, and green lacewings with those of sucking insects; and the chemical characteristics of the soils (Leite et al. 2006a) and

### Table 1. Hill’s diversity index, number of individuals, and number of species of sucking insects and their natural enemies per Caryocar brasiliense tree in 3 areas of Montes Claros, Minas Gerais, Brazil.

| Variable             | Cerrado | Anthropic area | Pasture | F    | P    |
|----------------------|---------|----------------|---------|------|------|
| Sucking insects      |         |                |         |      |      |
| Diversity index      | 3.81 ± 0.79 | 4.65 ± 0.46 | 3.54 ± 0.43 | —     | n.s. |
| No. of individuals   | 11.67 ± 2.59c | 44.75 ± 9.37b | 86.58 ± 5.88a | 38.778 | <0.0001 |
| No. of species       | 3.23 ± 0.44b | 3.83 ± 0.32a | 4.17 ± 0.50a | 8.278 | 0.0021 |
| Natural enemies      |         |                |         |      |      |
| Diversity index      | 7.47 ± 1.51 | 9.88 ± 0.63 | 7.35 ± 0.65 | —     | n.s. |
| No. of individuals   | 12.08 ± 0.94c | 44.83 ± 4.40b | 65.58 ± 5.86a | 73.827 | <0.0001 |
| No. of species       | 4.25 ± 0.53b | 5.50 ± 0.31ab | 7.25 ± 0.50a | 10.764 | 0.0006 |

Means (± SE) followed by the same letter in each row do not differ by the Tukey test (P > 0.05). Values of F and P were determined by ANOVA; n.s. = not significant by ANOVA; df = 22.
height and crown width of the plants (Leite et al. 2006a) with the numbers of sucking insects and their natural enemies. Results were subjected to analysis of variance (ANOVA) (P < 0.05) and simple regression analysis (P < 0.05) using the System of Statistical and Genetics Analysis of the Federal University of Viçosa. The effect of the areas on ecological indices and number of individuals per species of sucking insects and their natural enemies was tested with ANOVA (P < 0.05) and Tukey’s test (P < 0.05), carried out using the same software.

**Results**

In total, 1,728 leaves, 300 flowers (Jul–Sep), and 320 fruits (Sep–Jan) of *C. brasiliense* were evaluated during the 3 yr in the 3 areas. The diversity index of sucking insects and natural enemies was similar between areas. However, sucking insects and natural enemies were more abundant in the pasture than in the Cerrado. The number of species of sucking insects and their natural enemies was greatest in the pasture and smallest in the Cerrado (Table 1). One rare, 8 common, and 1 frequent species of sucking insects and 2 rare, 7 common, and 6 frequent species of natural enemies were found on *C. brasiliense* trees (Table 2).

The numbers of the Hemiptera *Aconophora* sp. (Membracidae) on fruit peduncles and *Dikrella caryocar* Coelho, Leite and Da-Silva in the anthropic area than in the other areas. On the other hand, aphids, whiteflies, and a membracid (unidentified) had larger populations in the anthropic area than in the other areas. The number of natural enemies *Crematogaster* sp. (Hymenoptera: Formicidae) was greatest on leaves, flowers, and fruits of *C. brasiliense* trees in the pasture than in other areas. The number of natural enemies *Crematogaster* sp. (Hymenoptera: Formicidae) was greatest on leaves, flowers, and fruits of *C. brasiliense* trees in the pasture than in the other areas. On the other hand, aphids, whiteflies, and a membracid (unidentified) had larger populations in the anthropic area than in the other areas (Table 3).

The number of natural enemies *Crematogaster* sp. (Hymenoptera: Formicidae) was greatest on leaves, flowers, and fruits of *C. brasiliense* trees in the pasture; those of *Epiophlops* sp. (Hemiptera: Geocorinae) bugs, *Neocalvia fulgurata* Mulsant (Coleoptera: Coccinellidae) lady beetles, and *Trybonia* sp. (Thysanoptera: Phlaeothripidae) thrips on leaves, and of spiders on flowers also were greatest in the anthropic area (Table 4). Numbers of *Pseudomymex termitarius* Smith (Hymenoptera: Formicidae) ants on leaves were greatest in the Cerrado, whereas numbers of *Camponotus novogranadensis* Mayr (Hymenoptera: Formicidae) ants, green lacewings (*Chrysoperla* sp.), spiders, and *Zelus armillatus* (Lepeletier and Serville) lady beetles (Hymenoptera: Coccinellidae) lady beetles on flowers also were greatest in the anthropic area (Table 4). *Holopothrips* sp. (Thysanoptera: Thripidae) had larger populations in the anthropic area than in the other areas.

### Table 2. Order, family, and species of arthropods and their feeding behavior and abundance observed on *Caryocar brasiliense* trees in Montes Claros, Minas Gerais, Brazil.

| Order          | Family       | Species                  | Feeding         | Abundance† |
|---------------|-------------|--------------------------|-----------------|------------|
| Coleoptera    | Carabidae   | *Colosoma* sp.           | predator       | rare-L     |
|               | Coccinellida| *Neocalvia fulgurata* Mulsant | predator       | common-L   |
| Hemiptera     | Aethaloniida| *Aethalium reticulatum* L. | leaves        | rare-L     |
|               | L.          | *Aethalium reticulatum* L. | flowers       | rare-L     |
|               | Aethaloniida| *Aethalium reticulatum* L. | leaves        | common-L   |
|               | L.          | *Aethalium reticulatum* L. | flowers       | common-L   |
|               | L.          | *Aethalium reticulatum* L. | leaves        | common-L   |
| Aphidoidea    | L.          | *Aethalium reticulatum* L. | leaves        | common-L   |
|               | L.          | *Aethalium reticulatum* L. | leaves        | common-L   |
|               | L.          | *Aethalium reticulatum* L. | leaves        | common-L   |
|               | L.          | *Aethalium reticulatum* L. | leaves        | common-L   |
|               | L.          | *Aethalium reticulatum* L. | leaves        | common-L   |
|               | L.          | *Aethalium reticulatum* L. | leaves        | common-L   |
|               | L.          | *Aethalium reticulatum* L. | leaves        | common-L   |
|               | L.          | *Aethalium reticulatum* L. | leaves        | common-L   |
|               | L.          | *Aethalium reticulatum* L. | leaves        | common-L   |

† L = Leaves, Fl = flowers, and Fr = fruits.

†‡ Spiders = *Cheiracanthium inclusum* (Hentz) (Thomisidae); *Parawixia reticularis* (Thomisidae); *Anelosimus* sp., *Aconophora* sp., *Chrysoperla* sp., *Trybonia* sp. (Thysanoptera: Phlaeothripidae), *Camponotus* novogranadensis (Hymenoptera: Formicidae) ants, *Zelus armillatus* (Lepeletier and Serville) lady beetles (Hymenoptera: Coccinellidae) lady beetles, and *Trybonia* sp. (Thysanoptera: Phlaeothripidae) thrips on leaves, and of spiders on flowers also were greatest in the anthropic area (Table 4). Numbers of *Pseudomymex termitarius* Smith (Hymenoptera: Formicidae) ants on leaves were greatest in the Cerrado, whereas numbers of *Camponotus novogranadensis* Mayr (Hymenoptera: Formicidae) ants, green lacewings (*Chrysoperla* sp.), spiders, and *Zelus armillatus* (Lepeletier and Serville) lady beetles (Hymenoptera: Coccinellidae) lady beetles on flowers also were greatest in the anthropic area (Table 4). *Holopothrips* sp. (Thysanoptera: Thripidae) had larger populations in the anthropic area than in the other areas.
Table 3. Numbers of sucking insects on leaves (L), flowers (Fl), and fruits (Fr) per Caryocar brasiliense tree in 3 areas of Montes Claros, Minas Gerais, Brazil.

| Sucking insects   | Cerrado     | Anthropic area | Pasture | F    | P      |
|-------------------|-------------|----------------|---------|------|--------|
| Aethalium reticulatum-Fl | 0.00 ± 0.00  | 0.00 ± 0.00    | 0.42 ± 0.33 | —    | n.s.   |
| Aethalium reticulatum-L  | 0.00 ± 0.00  | 0.00 ± 0.00    | 0.17 ± 0.11 | —    | n.s.   |
| Aconophora sp.-Fl | 0.00 ± 0.00  | 0.00 ± 0.00    | 1.83 ± 1.08 | —    | n.s.   |
| Aconophora sp.-L  | 0.00 ± 0.00  | 0.00 ± 0.00    | 10.33 ± 4.51a | 8.398 | 0.0020 |
| Aconophora sp.-Fr | 0.00 ± 0.00b | 0.00 ± 0.00b   | 3.00 ± 0.74a | 172.500 | <0.0001 |
| Frequenamia sp.-L | 0.58 ± 0.33  | 0.42 ± 0.14    | 1.17 ± 0.57 | —    | n.s.   |
| Edessa ruformarginata-L | 0.00 ± 0.00b | 0.00 ± 0.00b   | 0.42 ± 0.14a | 7.857  | 0.0027 |
| Membracidae-L   | 0.17 ± 0.11ab| 0.00 ± 0.00b   | 1.17 ± 0.57a | 4.930  | 0.0170 |
| Dikrella caryocar-L | 0.62 ± 2.00b | 5.83 ± 0.82b   | 6.75 ± 3.47a | 172.500 | <0.0001 |
| Pseudococcus sp.-L | 1.25 ± 0.44  | 3.08 ± 1.32    | 2.08 ± 1.42 | —    | n.s.   |
| Aphis gossypii-L | 3.08 ± 1.74b | 34.33 ± 8.72a  | 0.25 ± 0.17b | 30.977 | <0.0001 |
| Bemisia tabaci-L | 0.17 ± 0.11b | 0.67 ± 0.18a   | 0.17 ± 0.11b | 4.820  | 0.0184 |
| Mahanarva sp.-L | 0.00 ± 0.00b | 0.00 ± 0.00b   | 0.83 ± 0.27a | 11.714 | 0.0004 |

Means (± SE) followed by the same letter per row do not differ by the Tukey test (P > 0.05). Values of F and P were determined by ANOVA; n.s. = not significant by ANOVA; df = 22.

Discussion

The largest number of sucking insects and their natural enemies on C. brasiliense trees in the pasture (versus in the Cerrado and in the anthropic area) may be explained by a combination of factors. First, the pasture environment, in our study, with C. brasiliense trees, grass, and other trees and shrubs had a more diversified condition than a traditional pasture (grass only) (Leite et al. 2006a, 2011a), increasing the number of sucking insect species. Second, C. brasiliense trees presented wider and higher crowns (complexity in the structure) in the pasture than in the other 2 areas, increasing food resources (Leite et al. 2006a). Third, soil characteristics in the pasture were most favorable to C. brasiliense trees—increasing their crown and consequently their fruit production (Leite et al. 2006a, 2011a, 2012), which indirectly benefitted hemipteran herbivores and natural enemies. The large numbers of aphids, whiteflies, and mealybugs and their natural enemy green lacewings on C. brasiliense trees in the anthropic area may be due to its proximity to vegetable production areas (i.e., okra, tomato). Environmental complexity and host plant

Table 4. Numbers of natural enemies on leaves (L), flowers (Fl), and fruits (Fr) per Caryocar brasiliense tree in 3 areas of Montes Claros, Minas Gerais, Brazil.

| Natural enemies       | Cerrado     | Anthropic area | Pasture | F    | P      |
|-----------------------|-------------|----------------|---------|------|--------|
| Crematogaster sp.-Fl  | 1.58 ± 0.93b| 0.42 ± 0.19b   | 19.17 ± 3.56a | 45.703| <0.0001|
| Crematogaster sp.-Fr  | 0.25 ± 0.13b| 0.00 ± 0.00b   | 6.25 ± 1.99a | 14.755| <0.0001|
| Crematogaster sp.-L   | 6.33 ± 0.93b| 3.67 ± 0.80b   | 15.17 ± 2.40a | 14.214| 0.0002 |
| Pseudomyrmex termatarius-Fr | 0.00 ± 0.00  | 0.17 ± 0.11    | —      | n.s.   |
| Pseudomyrmex termatarius-L | 1.08 ± 0.14a | 0.42 ± 0.14b   | 0.67 ± 0.22ab | 4.724| 0.0197 |
| Cephalotes minutus-L  | 0.00 ± 0.00  | 0.17 ± 0.11    | —      | n.s.   |
| Dorymyrmex sp.-L      | 0.00 ± 0.00  | 0.17 ± 0.11    | —      | n.s.   |
| Camponotus novograndensis-L | 0.00 ± 0.00b | 0.33 ± 0.14a   | 0.00 ± 0.00b | 5.500| 0.0116 |
| Holothrips sp.-L      | 0.50 ± 0.15b| 1.67 ± 0.41a   | 1.58 ± 0.25a | 5.096 | 0.0152 |
| Trybonia intermedius + Trybonia mendesi-L | 0.42 ± 0.19b | 11.67 ± 1.52a  | 1.58 ± 0.74a | 7.511 | 0.0033 |
| Zelus armillatus-L    | 0.33 ± 0.18b| 21.00 ± 2.55a  | 1.08 ± 0.19b | 128.652| <0.0001 |
| Epipolus sp.-L        | 0.25 ± 0.13b| 0.19 ± 0.35a   | 43.223  | <0.0001 |
| Colosoma sp.-L        | 0.00 ± 0.00  | 0.25 ± 0.17    | —      | n.s.   |
| Neocalvia fulgurata-L | 0.00 ± 0.00b | 0.00 ± 0.00b   | 1.58 ± 0.74a | 7.511 | 0.0033 |
| Chrysoperla sp.-L     | 0.42 ± 0.19b| 11.67 ± 1.52a  | 0.00 ± 0.00b | 83.561| <0.0001 |
| Spiders-Fl            | 0.00 ± 0.00b| 0.42 ± 0.19a   | 5.013   | 0.0161 |
| Spiders-L             | 0.92 ± 0.22c | 5.67 ± 0.44a   | 2.08 ± 0.39b | 36.564| <0.0001 |

Means (± SE) followed by the same letter per row do not differ by the Tukey test (P > 0.05). Values of F and P were determined by ANOVA; n.s. = not significant by ANOVA; df = 22.
Fig. 1. Correlation of diversity indices, numbers of individuals, and numbers of species between sucking insects and their natural enemies; between number of sucking insects and total numbers of ants, green lacewings, predatory thrips, and lady beetles per *Caryocar brasiliense* tree in the 3 areas of Montes Claros, Minas Gerais, Brazil. Symbols represent the mean values.
Fig. 2. Correlation of soil pH, soil aluminum level, tree height, and crown width with diversity indices, numbers of individuals, and numbers of species of sucking insects and their natural enemies per *Caryocar brasiliense* tree in the 3 areas of Montes Claros, Minas Gerais, Brazil. Symbols represent the mean values.
attributes (such as architecture and nutritional quality) influence the diversity of arthropods, both phytophagous ones and natural enemies (Auslander et al. 2003; Espírito-Santo et al. 2007; Lazo et al. 2007; Leite et al. 2011b, 2012). The number of species associated with a given host in less complex environments may be low but with generally high population abundance, hence giving herbivores pest status (Landis et al. 2000; Gonçalves-Alvim & Fernandes 2001; Gratton & Denno 2003; Coyle et al. 2005).

Fig. 3. Correlation of soil pH, soil aluminum level, tree height, and crown width with numbers of Dikrella caryocar and Aphis gossypii individuals per Caryocar brasiliense tree in the 3 areas of Montes Claros, Minas Gerais, Brazil. Symbols represent the mean values.
The positive correlation between sucking insects on *C. brasiliense* plants with high aluminum level and acidic soils, except *Aphis gossypii* (Glover) (Hemiptera: Aphididae) (a pest of several crops), may be due to the loamier soil in the pasture than in the anthropic area (silt and compressed texture) and the Cerrado (sandy texture) (Leite et al. 2006a). Soils of the Cerrado are generally deep and loamy (excellent storage capacity for rainfall water) but poor in nutrients, rich in aluminum, and with low pH (Sousa & Lobato 2004). The soil in the pasture had higher levels of aluminum and lower pH values along with lower levels of calcium, potassium, and magnesium than soil in the anthropic area (Leite et al. 2006a). *Caryocar brasiliense* (Oliveira 1997; Leite et al. 2006a) and its native sucking insect species may have adapted to these conditions.

The greatest number of the predators *Z. armillatus*, *Holopothrips* sp., and spiders on *C. brasiliense* trees in the anthropic area might be due to higher number of leaves galled by *Eurytoma* sp. (Hymenoptera: Eurytomidae) in these trees than in trees of the other 2 areas (unpublished data). These predators preyed on galling insects that colonize up to 70% of leaf area with galls (Leite et al. 2009). *Eurytoma* sp. and aphids are very abundant on leaves of seedlings and mature *C. brasiliense* trees in the anthropic area (Leite et al. 2006b, 2007).

The positive correlation between natural enemies and sucking insects on *C. brasiliense* trees shows that mobile predators can respond to local increase in vegetation complexity and alternative prey to effectively suppress herbivores (Auslander et al. 2003). Ants can reduce infestations by *E. rufomarginata*, *Eunica bechina* Hewitson (Lepidoptera: Nymphalidae), *Prodiplosis florica* (Felt) (Diptera: Cecidomyiidae), and petiole gall insects (Hymenoptera: Chalcidoidea) on *C. brasiliense* (Freitas & Oliveira 1996; Oliveira 1997). Also, spiders, predator bugs and thrips, green lacewings, and lady beetles are important natural enemies in various ecosystems (Landis et al. 2000; Almeida et al. 2006; Mizell 2007; Oberg et al. 2008; Venturino et al. 2008). Spiders and invertebrate predators often have a high population density in complex vegetation (plant architecture) independent of prey (Landis et al. 2000). High population density of these natural enemies was also attributed to microclimate or reduction of cannibalism and intraguild competition (Langellotto 2002).

A more diverse environment and, principally, higher structure of plant crown (complexity of the architecture) favored populations of sucking insects and of their natural enemies. The positive effect of high aluminum levels and acidic soils on sucking insects (except aphids) indicates the adaptation of these species to the Cerrado conditions. Besides, it reinforces the importance of sucking insects in arboreal systems of the Brazilian Cerrado and the necessity of studying their population dynamics.

Fig. 4. Correlation between tree height and crown width with total numbers of ants, predator thrips, and lady beetles per *Caryocar brasiliense* tree in the 3 areas of Montes Claros, Minas Gerais, Brazil. Symbols represent the mean values.
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