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Authors: Leite, Germano Leão Demolin, Veloso, Ronnie Von Dos Santos, Zanuncio, José Cola, Almeida, Chrystian Iezid Maia E, Ferreira, Paulo Sérgio Fiúza, et al.

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HABITAT COMPLEXITY AND *CARYOCAR BRASILIENSE* HERBIVORES (INSECTA: ARACHNIDA: ARANEAE)

Germano Leão Demolin Leite[1*], Ronnie Von Dos Santos Veloso[2], José Cola Zanuncio[2], Chrystian Iezid Maia E Almeida[1], Paulo Sérgio Fiúza Ferreira[2], Geraldo Wilson Fernandes[3] and Marcus Alvarenga Soares[4]

[1]Insetário G.W.G. de Moraes, ICA/UFMG, CP: 135. Montes Claros, MG, Brasil

[2]Departamento de Biologia Animal/BIOAGRO, Universidade Federal de Viçosa, 36571-000, Viçosa, Minas Gerais State, Brazil

[3]Departamento de Biologia Geral, Universidade Federal de Viçosa, 36571-000, Viçosa, Minas Gerais State, Brazil

[4]Programa de Pós-graduação em Producão de Plantas, Universidade Federal dos Vales do Jequitinhonha e Mucuri, Diamantina, Minas Gerais State, 39100-000, Brazil

*Corresponding author; E-mail: gldleite@ig.com.br

Abstract

Caryocar brasiliense Camb. (Malpighiales: Caryocaraceae) trees have a wide distribution in the cerrado. This plant is protected by federal laws and is left in deforested areas of the cerrado. This situation increases the damage to leaves, flowers, and fruits from chewing insects. We studied the effect of habitat complexity and plant architecture on the diversity and abundance of the Lepidoptera, Coleoptera, and Hymenoptera herbivores and their predators on trees of *C. brasiliense* in cerrado, pasture, and on the Campus of the Federal University of Minas Gerais. We observed 13 rare, 2 common, and 1 constant species of herbivores insects; and 3 rare, 8 common, and 1 constant species of predators on trees. Higher diversities and number of species of herbivores insects and their predators were observed in pasture than in the cerrado and on the campus of the Federal University of Minas Gerais. Herbivorous insects were most abundant in pasture and least abundant on the university campus. Predators were most abundant in pasture and least abundant in the cerrado. Ants, spiders, and predatory bugs are important in the reduction of the defoliators and leaf miners insects. The percentages of defoliation and populations of defoliators and ants were higher on *C. brasiliense* trees with wider crowns. We found a positive correlation of soil aluminum concentration with percent defoliation and numbers of lepidopteran leaf miners. On the other hand, increased soil pH was correlated with reduction in percent defoliation and numbers of lepidopteran leaf miners.

Key Words: beetles, caterpillars, entomology, predators, pequi

Resumen

Los árboles de *Caryocar brasiliense* Camb. (Malpighiales: Caryocaraceae) tienen una amplia distribución en lo cerrado. Esta planta está protegida por las leyes federales y se deja en las áreas deforestadas de lo cerrado. Esta situación aumenta el daño a las hojas, flores y frutos de los insectos masticadores. Se estudió el efecto de la complejidad del hábitat y la arquitectura de la planta en la diversidad y abundancia de los lepidópteros, coleópteros y himenópteros herbívoros y sus predadores en los árboles de *C. brasiliense* en el cerrado, pastizales, y en el campus de la universidad. Observamos 13 raras, 2 comunes, y 1 especie constante de insectos herbívoros, y 3 raras, 8 comunes, y 1 especie constante de los predadores en los árboles. Las diversidades más altas y el número de especies de insectos fitófagos y sus predadores se observaron en los pastos que en el cerrado y en el campus de la universidad. Los insectos fitófagos fueron más abundantes en pastos y menos abundantes en el campus universitario. Los predadores son más abundantes en pastos y menos abundantes en el cerrado. Las hormigas, arañas y los insectos depredadores son importantes en la reducción de los defoliadores e insectos minadores de las hojas. El porcentajes de defoliación, y poblaciones del defoliantes y las hormigas son mayores en árboles de *C. brasiliense*, una más ancha corona. Hemos encontrado una correlácion positiva de la concentración de aluminio en el porcentaje de defoliación y el número de minadores lepidópteros de hojas. Por otro lado, el pH del suelo correlacionado negativamente el porcentaje de defoliación y el número de minadores lepidópteros de hojas.

Palabras Clave: escarabajos, orugas, entomología, predadores, pequi

The cerrado occupies about 23% of the territory of Brazil (Da Silva & Bates 2002). It is characterized by a high diversity of plants and insects and contains a high degree of endemism (Bridgewater et al. 2004). Naturally, the cerrado is formed by a complex mosaic of phytophysiographies that range from open cerrado formations (*campo limpo*) up to tall and woody forests of 10-15 m tall called *Cerradão* (Oliveira & Marquis 2002). Due to increasing threats to its biodiversity, the cerrado has been designated a biodiversity hotspot (Myers et al. 2000). The cerrado's primary economic use is for grain and cattle production (Aguiar & Camargo 2004), as well as reforestation with exotic species, primarily *Eucalyptus* (Zanuncio et al. 2002). Several governmental mechanisms and incentives have devastated the cerrado in the last 5 decades, and have left only 20% in an unmodified or pristine condition (Klink & Machado 2005). In southeastern Brazil large patches of this rich cerrado are seen immersed in a matrix of agriculture (primarily soybean and sugar cane), cattle farms and cities (urbanization).

Caryocar brasiliense Camb. (Malpighiales: Caryocaraceae) is widely distributed in this region (Brandão & Gavilanes 1992; Bridgewater et al. 2004; Leite et al. 2006a) and can reach over 10 m in height and 6 m in canopy width (Leite et al. 2006a). The leaves of *C. brasiliense* are alternate, trifoliate and have a high trichome density; the flowers are hermaphrodite but mostly cross pollinated (Araújo 1995). Fruit production is annual, and *C. brasiliense* blooms between Jul and Sep (dry period) with fructification from Oct through Jan (rainy season) (Leite et al. 2006a). The fruit is a drupe with 1-4 seeds, weighing 158.49 ± 8.14 g (fresh weigh) and with a volume of 314.90 ± 20.93 cm^3 (Leite et al. 2006a). Its fruits have internal mesocarp rich in oil, vitamins, and proteins, and contain many compounds of medicinal importance. Moreover, it is used by humans for food, production of cosmetics, 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 represents the main source of income of many communities (Leite et al. 2006a).

Due to protection by federal law, *C. brasiliense* trees are left in deforested areas of the cerrado. The production and natural regeneration of *C. brasiliense* has been impaired by the practice of only conserving as forest or cerrado reserve areas the most impoverished areas where sandy or rocky soils do not allow its survival or colonization (Leite et al. 2006a). This is the scenario found in the northern part of Minas Gerais State (Leite et al. 2006a). Coleoptera, Lepidoptera, and Hymenoptera are the most abundant orders of chewing insects in the cerrado (Pinheiro et al. 2002; Zanetti et al. 2003; Zanuncio et al. 2002). Isolated *C. brasiliense* individuals in the agro-landscape suffer increased leaf, flower, and fruit damage from these insect herbivores group (personal communication from collectors of *C. brasiliense* fruits). Despite the biological and social importance of *C. brasiliense*, its herbivores are still poorly known (Araújo 1995) and the identification of many of them has been hampered due to the lack of taxonomic specialists (Freitas & Oliveira 1996; Oliveira 1997; Lopes et al. 2003; Boiça et al. 2004, Leite et al. 2011 a,b,c). Furthermore, long term data on *C. brasiliense* herbivore dynamics are unknown to date.

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

We test, for the first time, three hypotheses —complex environments, host plant attributes, and soil characteristics—in relation the diversity and abundance of Lepidoptera, Coleoptera, and Hymenoptera herbivores and their predators on *C. brasiliense* individuals under 3 different areas. We studied plants under 3 very different habitat conditions: i) preserved cerrado, ii) cerrado cleaned for pasture, and iii) cerrado converted to urban development (a university Campus).

Material and Methods

Study Sites

The study was done in the municipality of Montes Claros, in the state of Minas Gerais, Brazil, during 3 consecutive yr (Jun 2007 through Jun 2010). The region has dry winters and rainy summers, and is classified as climate Aw: tropical savanna according to Köppen (Vianello & Alves 2000). Three areas were studied: 1) strict sense cerrado (S 16° 44' 55.6" W 43° 55' 7.3", at 943 m asl and containing dystrophic yellow red oxisol with sandy texture); 2) pasture, formerly cerrado vegetation (S 16° 46' 16.1" W 43° 57' 31.4" at 940 m asl and containing red dystrophic yellow oxisol with loamy texture), and 3) campus of the "Instituto de Ciências Agrárias da Universidade Federal de Minas Gerais (ICA/UFMG)" (S 16° 40' 54.5" W 43° 50' 26.8", at 633m asl and containing dystrophic red oxisol with medium texture). For detailed description of the sites see Leite et al., 2006a, 2011a.

The strict sense cerrado (a species-rich dense scrub of shrubs and trees, 8-10 m high, with a dense understory) is more typical of the cerrado than grassland open forms (Ribeiro & Walter 1998; Durigan et al. 2002). The soil covering of the cerrado area was grass (44.87%) and bare soil (55.13%), on which were found an average number per ha of the these plants: shrubs (5.78), small trees (23.51), tall trees (8.76); and *C. brasiliense* trees (17.00). The soil covering of the pasture area was *Brachiaria decumbens* (Stapf) grass (84.19%) and bare soil (15.81%), on which were found an average number per ha of the these plants: shrubs (0.19), small trees (4.76), tall trees (2.76) and *C. brasiliense* trees (42.30). The soil covering of the university campus was *Paspalum notatum* grass (100%) on which were found with 100 *C. brasiliense* trees per hectare (see Leite et al. 2006a, 2011a), and there were nearby vegetable gardens (~300 m).

Adult *C. brasiliense* trees in the cerrado were 4.07 ± 0.18 m high (average ± SE) and had crown widths of 2.87 ± 0.13 m; in the pasture these plants were 5.20 ± 0.18 m high with crown widths of 3.96 ± 0.14 m, while in the university campus they were 3.79 ± 0.15 m high with crown widths of 1.66 ± 0.13 m (Leite et al. 2006a, 2011a).

Study Design

The design was completely randomized with 12 replicates (1 tree/replicate) and 3 treatments (areas). In both the cerrado area and the pasture area, we walked (~600 m) in each area in a straight line, and at every 50 m we collected data on a *C. brasiliense* tree. Adult trees of *C. brasiliense* (producing fruits) were randomly sampled in each collection in the cerrado and pasture areas, but on the lawn of the university campus the same 12 trees were sampled every time. We collected data according to this design in 3 consecutive yr to capture the overwhelming majority of species of insects (i.e., rare species), since in a given yr some of them might not occur.

The percent defoliation by caterpillars and beetles, numbers of lepidopteran and coleopteran defoliators, damage to flowers by Hymenoptera, scraping and boring of fruits by insects and status of their arthropod predators were evaluated monthly in the morning by direct observation of 4 leaves, 4 flowers and 4 fruits per tree in each area during each of the 3 yr. Defoliation was determined visually by estimating the percent of leaf area lost on a scale from 0-100% with increments of 5% of the total leaf area removed (Sastawa et al. 2004; Mizumachi et al. 2006). Insects present in the evaluated parts (leaves, flowers, and fruits) of *C. brasiliense* were collected with tweezers, a brush, or with an aspirator and preserved in vials with 70% alcohol for identification. Evaluations in the 3 areas involved a total of 1,728 leaves, 300 flowers (Jul-Sep), and 320 fruits (Sep-Jan) during the 3 yr.

The abundances of herbivore and natural enemy individuals, species richness and diversity were calculated per tree in each area. Hill's formula (Hill 1973) was used to calculate diversity, and the Simpson index was used to calculate the abundance and richness of species (Townsend et al. 2006; Lazo et al. 2007). We calculated the percentage of samples that contained each species. The presence of each species was represented by 1 and absence by 0. Further, we used a method adapted by Siqueira et al. (2008 to classify the species of herbivores and predators in the samples as: a) constant (presence ≥ 50%), b) common (10% < presence ≤ 49%), and c) rare (presence ≤ 10%).

Statistical Analyses

Correlations of numbers of individuals and species of herbivorous insects with the diversity index, and numbers of individuals and species of predators were subjected to analysis of variance (ANOVA) ($P < 0.05$) and simple regression analysis ($P < 0.05$). We made the same analysis with each species of predator, with each insect herbivore species and its damage, as well as chemical characteristics of the soils and height and crown of plants (see Leite et al. 2006a). The effects of the 3 different areas on the ecological indices, and number of individuals of each species of herbivorous insect and their predators were transformed to $\sqrt{x + 0.5}$, tested with ANOVA ($P < 0.05$) , and subsequently with Tukey's test ($P < 0.05$).

Results

We observed 13 rare, 2 common, and 1 constant species of herbivorous insects; and 3 rare, 8 common, and 1 constant species of arthropod predators on *C. brasiliense* trees (Table 1). Higher diversities and number of species of herbivores insects and their predators were observed on the pasture than in the cerrado and on the university campus. Herbivorous insects were most abundant in pasture and least abundant on the university campus (Table 2). Predators were most abundant on the pasture and least abundant in the cerrado (Table 3).

The numbers of bored fruits and numbers and percentages of scraped fruits were greater on the pasture than in the other areas. We observed higher numbers of damaged flowers and lepidopteran leaf miners on the pasture than on the university campus. Percentages of defoliation and bored fruits were higher on the pasture and in the cerrado than on the campus. However, the number of *Eunica bechina* (Lepidoptera: Nymphalidae) caterpillars was greater on the leaves on the university campus than at the other 2 sites. A larger number of the *Naupactus* sp.3 (Coleoptera: Curculionidae) beetles was observed on

TABLE 1. ORDERS AND FAMILIES OF SPECIES OBSERVED ON *CARYOCAR BRASILIENSE* TREES, THE OBJECTS ON WHICH THEY FED AND THE FREQUENCIES OF THEIR OCCURRENCE DURING THE DAY. STUDY CONDUCTED AT MONTES CLAROS, MINAS GERAIS STATE, BRAZIL.

Order	Family	Species	Feeding	Occurrence
Coleoptera	Alticidae	*Oedionychus* sp.	Leaves	Rare-L
	Carabidae	*Calosoma* sp.	Predator	Rare-L
	Chrysomelidae	*Diabrotica speciosa* Germar	Leaves	Rare-L
	Coccinellidae	*Neocalvia fulgurata* Mulsant	Predator	Rare-L
	Curculionidae	*Naupactus* sp.1	Fruits	Rare-Fr
			Leaves	Rare-L
		Naupactus sp.2	Fruits	Rare-Fr
		Naupactus sp.3	Leaves	Rare-L
		Rhinochenus stigma (L.)	Leaves	Rare-L
	Elateridae	*Apoptus* sp.	Leaves	Common-L
	Tenebrionidae	*Camaria* sp.	Leaves	Rare-L
Lepidoptera	NI*	NI - leaf miner	Leaves	Constant-L
	Arctiidae	NI	Leaves	Rare-L
	Ctenuchiidae	NI	Leaves	Rare-L
	Nymphalidae	*Eunica bechina* Talbot	Leaves	Rare-L
	Oecophoridae	NI	Leaves	Rare-L
	Sesiidae	*Carmenta* sp.	Fruits	Common-Fr
Hemiptera	Geocoridae	*Epipolops* sp.	Predator	Common-L
	Reduviidae	*Zelus armillatus* (Lep. and Servi)	Predator	Common-L
Hymenoptera	Apidae	*Trigona spinipes* Fabr.	Pollinator	Rare-Fl
	Formicidae	*Crematogaster* sp.	Generalist	Constant-L
			Generalist	Common-Fl
			Generalist	Common-Fr
		Pseudomyrmex termitarius Smith	Predator	Common-L
			Predator	Rare-Fr
Neuroptera	Chrysopidae	*Chrysoperla* sp.	Predator	Common-L
Orthoptera	Tettigoniidae	*Oxyprora flavicornis* Redtenb.	Leaves	Rare-L
Thysanoptera	Phlaeothripidae	*Holopothrips* sp.	Predator	Common-L
		Trybonia intermedius Bagnall	Predator	Common-L
		Trybonia mendesi Moulton	Predator	Common-L
Araneae	**	Complex of spiders	Predator	Common-L
				Rare-Fl

*NI = none identified. **complex of spiders = *Cheiracanthium inclusum* Hentz (Miturgidae); *Peucetia rubrolineata* (Keyserling) (Oxyopidae); *Anelosimus* sp., *Achaearanea hirta* (Taczanowski) (Theridiidae); *Gastromicans albopilosa* Simon, *Chira bicirculigera* Soares and Camargo, *Rudra humilis* Mello-Leitão, *Thiodina melanogaster* Mello-Leitão and *Lyssomanes pauper* Galiano (Salticidae); *Dictyna* sp. and sp.1 (Dictynidae); *Tmarus* sp. and sp.1 (Thomisidae); *Argiope argentata* (Fabr.), *Gasteracantha cancriformes*, *Argiope* sp., *Parawixia* sp. and sp.1 (Araneidae); and Anyphaenidae. L = leaves, Fl = flowers, and Fr = fruits.

TABLE 2. HILL'S DIVERSITY INDEX, NUMBERS OF INDIVIDUALS AND SPECIES OF PREDATORS AND HERBIVOROUS INSECTS PER OF *CARYOCAR BRASILIENSE* TREE IN 3 ECOLOGICALLY DIFFERENT AREAS AT MONTES CLAROS, MINAS GERAIS STATE, BRAZIL.

Variables	Cerrado	Campus	Pasture	*F*	*P*
		Predatory arthropods			
Diversity index	8.77 ± 1.72 b	9.09 ± 0.69 b	15.24 ± 1.09 a	9.839	< 0.0009
No. of individuals	11.70 ± 0.89 c	43.60 ± 4.75 b	65.00 ± 5.70 a	44.799	< 0.0001
No. of species	4.75 ± 0.62 b	5.17 ± 0.32 b	9.08 ± 0.54 a	40.964	< 0.0001
		Herbivorous insects			
Diversity index	2.23 ± 0.23 b	3.77 ± 0.91 b	6.05 ± 0.52 a	11.464	< 0.0004
No. of individuals	17.40 ± 2.23 b	1.60 ± 0.28 c	36.80 ± 3.53 a	56.852	< 0.0001
No. of species	2.67 ± 0.51 b	1.83 ± 0.36 b	6.08 ± 0.84 a	31.178	< 0.0001

Means within a row followed by the same letter (average ± SE) are not different by Tukey's test ($P < 0.05$). Values of F and P were obtained by ANOVA; dfs of treatments, blocks, and errors were 2, 11, and 22, respectively.

TABLE 3. PHYTOPHAGES AND THEIR DAMAGES PER TREE OF *CARYOCAR BRASILIENSE* IN 3 ECOLOGICALLY DIFFERENT AREAS AT MONTES CLAROS, MINAS GERAIS STATE, BRAZIL.

Herbivores	Cerrado	Campus	Pasture	*F*	*P*
Bored fruits	0.60 ± 0.41 b	0.00 ± 0.00 b	6.70 ± 0.98 a	49.845	< 0.0001
Scraped fruits	0.33 ± 0.18 b	0.00 ± 0.00 b	20.60 ± 1.50a	449.276	< 0.0001
Damaged flowers	0.83±0.74 ab	0.00 ± 0.00 b	1.60 ± 0.25 a	7.424	< 0.0034
% defoliation	3.45 ± 0.16 a	0.46 ± 0.05 b	3.43 ± 0.23 a	261.013	< 0.0001
% bored fruits	9.80 ± 4.20 a	0.00 ± 0.00 b	15.22 ± 2.15 a	9.936	< 0.0001
% scraped fruits	6.86 ± 3.43 b	0.00 ± 0.00 b	33.98 ± 2.75 a	11.436	< 0.0001
% damaged flowers$^{n.s.}$	0.67 ± 0.59	0.00 ± 0.00	1.43 ± 0.50	2.877	0.0776
Naupactus sp.1-L$^{n.s.}$	0.20 ± 0.11	0.00 ± 0.00	0.50 ± 0.25	2.223	0.13199
Naupactus sp.1-Fr$^{n.s.}$	0.00 ± 0.00	0.00 ± 0.00	0.10 ± 0.08	1.435	0.25960
Naupactus sp.2-Fr$^{n.s.}$	0.00 ± 0.00	0.00 ± 0.00	0.10 ± 0.08	1.435	0.25960
Naupactus sp.3-L	0.00 ± 0.00 b	0.40 ± 0.13 ab	1.40 ± 0.60 a	5.147	< 0.0147
Apoptus sp.-L$^{n.s.}$	0.40 ± 0.13	0.40 ± 0.22	0.70 ± 0.17	0.980	0.4579
Rhynochenus stigma-L$^{n.s.}$	0.10 ± 0.08	0.00 ± 0.00	0.30 ± 0.12	2.750	0.08590
Oxyprora flavicornis-L$^{n.s.}$	0.00 ± 0.00	0.00 ± 0.00	0.10 ± 0.08	1.435	0.25960
Lepidoptera miners-L	15.90 ± 1.85 b	0.00 ± 0.00 c	25.10 ± 3.05 a	109.276	< 0.0001
Eunica bechina-L	0.00 ± 0.00 b	0.60 ± 0.13 a	0.20 ± 0.11 b	8.844	< 0.0015
Ctenuchiidae-L$^{n.s.}$	0.00 ± 0.00	0.00 ± 0.00	0.20 ± 0.11	1.435	0.25960
Oecophoridae-L$^{n.s.}$	0.10 ± 0.08	0.00 ± 0.00	0.10 ± 0.08	0.673	0.5983
Arctiidae-L$^{n.s.}$	0.00 ± 0.00	0.00 ± 0.00	0.10 ± 0.08	1.435	0.25960
Camaria sp.-L$^{n.s.}$	0.00 ± 0.00	0.00 ± 0.00	0.10 ± 0.08	1.435	0.25960
Oedionychus sp.-L$^{n.s.}$	0.00 ± 0.00	0.00 ± 0.00	0.10 ± 0.08	1.435	0.25960
Diabrotica speciosa-L$^{n.s.}$	0.00 ± 0.00	0.20 ± 0.11	0.10 ± 0.08	1.435	0.25960
Trigona spinipes-Fl$^{n.s.}$	0.10 ± 0.08	0.00 ± 0.00	0.90 ± 0.75	1.265	0.30192

Means followed by the same letter (± SE) in the same row are not different by Tukey's test ($P < 0.05$). Values of *F* and *P* were obtained by ANOVA. n.s. = non significant by ANOVA; dfs of treatments, blocks, and errors were 2, 11, and 22, respectively. L = leaves, Fl = flowers, and Fr = fruits.

the leaves of *C. brasiliense* in the pasture than in the cerrado (Table 3).

In the case of predators, *Crematogaster* sp. (Hymenoptera: Formicidae) were most abundant on the leaves, flowers, and fruits in the pasture. *Epipolops* sp. (Hemiptera: Geocoridae), ladybeetles, and *Trybonia intermedius* Bagnall and *T. mendesi* Moulton (Thysanoptera: Phlaeothripidae) presented the highest abundance on the leaves of *C. brasiliense* in the pasture. *Pseudomyrmex termitarius* (Hymenoptera: Formicidae) had the highest abundance on the leaves in the cerrado. *Zelus armillatus* (Hemiptera: Reduviidae), green lacewing, and spiders on the leaves of *C. brasiliense* were most abundant on the university campus. *Holopothrips* sp. (Thysanoptera: Phlaeothripidae) were least abundant on the leaves of *C. brasiliense* in the cerrado (Table 4).

We observed a positive correlation of number of species of herbivores insects with number of species of predators and ants with damaged fruits (Fig. 1). But no correlation was detected between numbers of individuals of predators with numbers of individuals of herbivores insects (Fig. 1). However, higher species diversity of predators decreased the species diversity of herbivores insects. Higher number of ants, predatory bugs and spiders decreased the number of lepidopteran leaf miners and percent defoliation (Figs. 1 and 2). We did not detect a correlation between predatory thrips, ladybeetles, and *Chrysoperla* sp. with percent defoliation and lepidopteran leaf miners (Fig. 2). We found a positive correlation of soil aluminum concentration with percent defoliation and numbers of lepidopteran leaf miners. On the other hand, increased soil pH was correlated with reduction in percent defoliation and numbers of lepidopteran leaf miners. On *C. brasiliense* trees with wider crowns the percentages of defoliation, and numbers of defoliators were greater than on trees with narrow crowns; and ants had higher populations on *C. brasiliense* trees with wider crowns than on tress with narrow crowns (Fig. 3).

DISCUSSION

The larger species diversity of herbivores (i.e., coleopteran and lepidopteran species), and consequently their predators, on *C. brasiliense* trees on the pasture than in the cerrado and on the university campus may be explained by a combination of factors. Firstly, the pasture environment included *C. brasiliense* trees, grass and other trees and shrubs (Leite et al. 2006a, 2011a). Secondly *C. brasiliense* trees presented wider crowns with more complex structures on the pasture than on

TABLE 4. PREDATORS PER TREE OF *CARYOCAR BRASILIENSE* IN 3 AREAS AT MONTES CLAROS, MINAS GERAIS STATE, BRAZIL.

Predators	Cerrado	Campus	Pasture	*F*	*P*
Crematogaster sp.-L	6.40 ± 0.93 b	3.60 ± 0.93 b	15.20 ± 2.40a	13.637	<0.0001
Crematogaster sp.-Fl	1.60 ± 0.93 b	0.40 ± 0.22 b	19.20 ± 3.56 a	45.468	<0.0001
Crematogaster sp.-Fr	0.20 ± 0.11 b	0.00 ± 0.00 b	6.30 ± 1.99a	15.057	<0.0001
Pseudomyrmex termitarius-L	1.10 ± 0.14 a	0.20 ± 0.11 b	0.60 ± 0.22 b	10.596	<0.0006
P. termitarius-Fr n.s.	0.00 ± 0.00	0.00 ± 0.00	0.10 ± 0.08	1.435	0.25960
Spiders-L	0.90 ± 0.23 c	5.60 ± 0.53 a	2.10 ± 0.39 b	35.411	<0.0001
Spiders-Fl n.s.	0.00 ± 0.00	0.00 ± 0.00	0.30 ± 0.17	2.883	0.07724
Zelus armillatus-L	0.30 ± 0.18 b	20.40 ± 2.84 a	1.10 ± 0.19 b	117.601	<0.0001
Epipolops sp.-L	0.20 ± 0.11 b	0.00 ± 0.00 b	1.90 ± 0.34 a	47.515	<0.0001
Neocalvia fulgurata-L	0.00 ± 0.00 b	0.00 ± 0.00 b	1.50 ± 0.74 a	6.437	<0.0063
Chrysoperla sp.-L	0.30 ± 0.17 b	11.80 ± 1.65 a	0.00 ± 0.00 b	68.927	<0.0001
Calosoma sp.-L n.s.	0.00 ± 0.00	0.00 ± 0.00	0.20 ± 0.16	1.435	0.25960
Holopothrips sp.-L	0.40 ± 0.13 b	1.60 ± 0.44 a	1.60 ± 0.25 a	5.427	<0.0121
Trybonia sp.-L	0.30 ± 0.17 b	0.00 ± 0.00 b	14.90 ± 3.89 a	53.481	<0.0001

Means followed by the same letter (± SE) in the same row are not different by the test of Tukey ($P < 0.05$). Values of F and P were obtained by ANOVA. n.s. =non significant by ANOVA. *df's* of treatments, blocks, and errors were 2, 11, and 22, respectively. L = leaves, Fl = flowers, and Fr = fruits.

the other 2 areas (Leite et al. 2006a). Thirdly, the soil characteristics in the pasture were more favorable to *C. brasiliense* trees (Leite et al. 2006a), and thereby indirectly favoring the lepidopteran and coleopteran herbivores and their predators.

Both habitat complexity and host-plant attributes (such as architecture, and nutritional quality) influence the diversity of phytophagous and predaceous arthropods (Auslander et al. 2003; Espírito Santo et al. 2007). Although in less complex environments the number of species associated with a given host species may be lower, abundance of each species is generally higher, increasing the likelihood that herbivores of economically valuable plants will become significant pest (Landis et al. 2000; Gonçalves-Alvim & Fernandes 2007; Gratton & Denno 2003; Coyle et al. 2005; Lazo et al. 2007). Mobile predators could respond to local increases in vegetation complexity and to the presence of alternative prey and effectively suppress herbivores (Auslander et al. 2003).

The higher populations of Coleoptera and Lepidoptera species and their predators (i.e., ants) on *C. brasiliense* trees with wider crowns may be strongly influenced by wind currents especially on the pasture. Leite et al. (2006a) observed the same results, but in relation the production of fruits on *C. brasiliense*. The period of blooming (Aug-Sep) of *C. brasiliense* trees occurs during the period with stronger winds, which results in higher production of fruits on trees with wider crowns because they are better protected from wind, especially on the pasture (Leite et al. 2006a). Ants can reduce *E. bechina* infestations as well as *Edessa rufomarginata* De Geer (Hemiptera: Pentatomidae), *Prodiplosis floricola* Felt (Diptera: Cecidomyiidae) and petiole gall insects (Hymenoptera: Chalcidoidea) on *C. brasiliense* (Freitas & Oliveira 1996; Oliveira 1997). A similar reduction of beetle and caterpillars defoliators and lepidopteran leaf-miners by ants was observed on *C. brasiliense* trees as well as with predatory bugs and spiders. Spiders and predatory bugs are also important in other ecosystems (Landis et al. 2000; Almeida et al. 2006; Mizell 2007, Oberg et al. 2008, Venturino et al. 2008). Spiders and invertebrate predators produce higher densities in more complex vegetation (plant architecture) independently of prey (Landis et al. 2000). This was attributed to microclimate or to reduction of cannibalism and intraguild competition (Langellotto 2002).

The highest number of the predators, *Z. armillatus*, *Holopothrips* sp., and spiders, in *C. brasiliense* trees on the university campus might be due to these trees having more leaves galled by *Eurytoma* sp. (Hymenoptera: Eurytomidae) than in the other 2 areas. Leite et al. (2009) observed these predators attacking this galling insect on *C. brasiliense*. In the case of green lacewings, the higher number observed on the university campus may be due to the large number of *Aphis gossypii* Glover (Hemiptera: Aphididae) in this area because of its proximity to a vegetable production area (i.e., okra). *Eurytoma* sp. and *A. gossypii* were very abundant on the leaves both of seedlings and adult of *C. brasiliense* on the university campus area (Leite et al. 2006b, 2007). The low numbers of coleopteran and lepidopteran defoliators on the campus may have been caused by competition for food and space with galling insects and aphids in this area. However, more research is needed to elucidate this hypothesis. Competition between defoliators and other phytophagous insects (gall-formers, aphids, leafhoppers, miners and mites) and natural enemies shows the importance of this

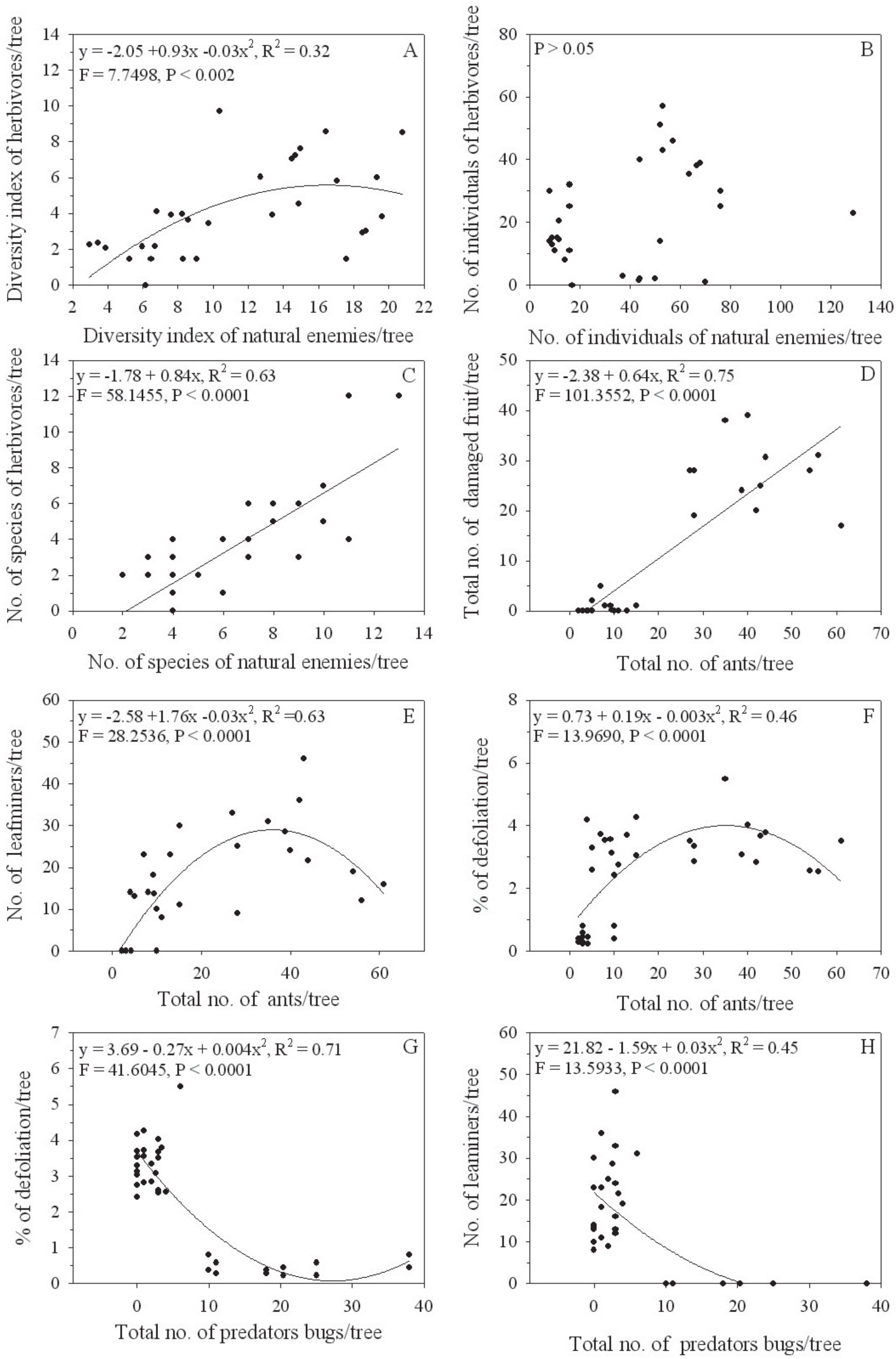

Fig. 1. Relationships between density and diversity of various phytophagous and predaceous arthropods and damage to *Caryocar brasiliense* trees in Montes Claros, Minas Gerais State, Brazil. Samples = 36.

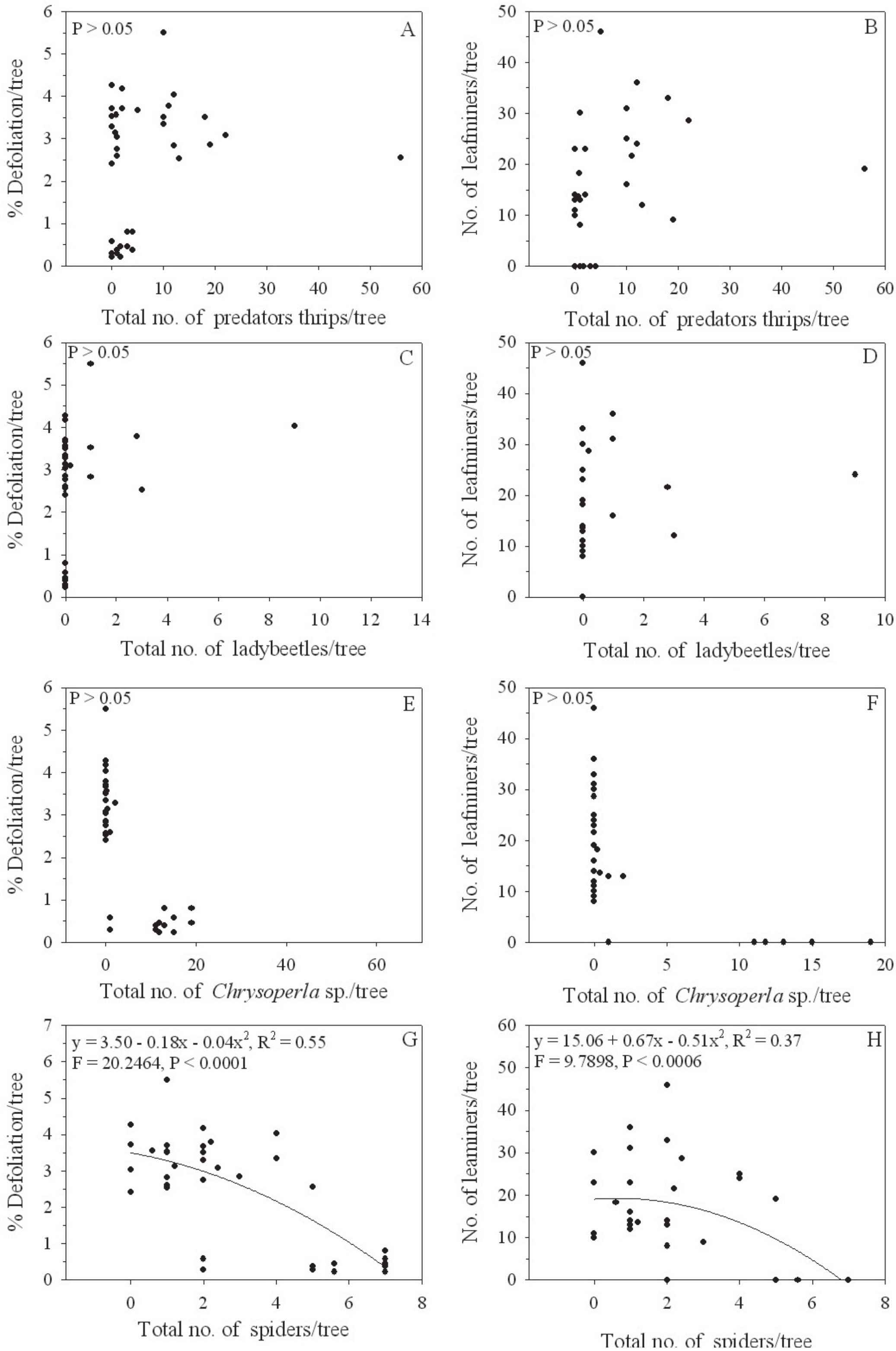

Fig. 2. Relationships between abundance of phytophagous and predaceous arthropods on *Caryocar brasiliense* trees in Montes Claros, Minas Gerais State, Brazil. Samples = 36.

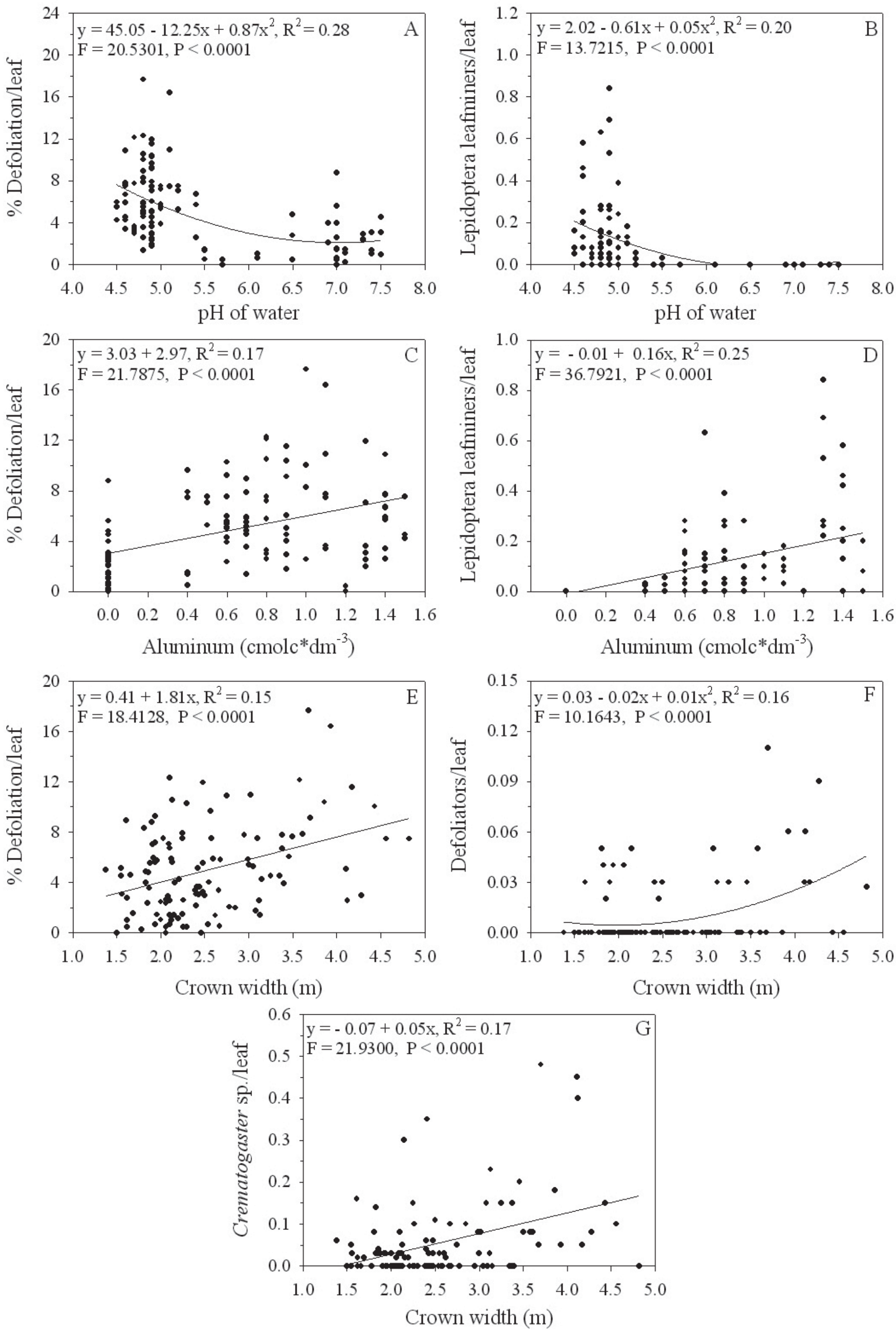

Fig. 3. Relationships between soil and tree attributes and phytophagous and predaceous arthropods on *Caryocar brasiliense* trees in Montes Claros, Minas Gerais State, Brazil. Samples = 108.

last group on host-plants in the tropics (Morris et al. 2004). The study of food webs is complex due to interactions among host plants, phytophagous insects, predators, parasitoids, and soil and climatic conditions (Gratton & Denno 2003). Few studies have examined food webs in complex ecosystems such as the cerrado (Marquis et al. 2001; Gratton & Denno 2003; Morris et al. 2004).

The presence of nectaries on leaves, flowers, and sugary secretions of damaged fruits by insects may explain the correlation between higher numbers of ants and reduction of defoliation by beetles, caterpillars and leaf mining by Lepidoptera. Spatial distributions of larvae that produce substances attractive to ants and tending ants were strongly aggregated, suggesting an influence of ants on the oviposition or larval survival of this group of herbivores (Kaminski 2008; Sendoya et al. 2009).

Finally, the lepidopteran and coleopteran defoliators and lepidopteran leaf miners found on *C. brasiliense* plants were correlated with higher soil aluminum levels and acidity. The soil of the pasture was loamier than that of the university campus (silt and compressed texture), and that of the cerrado (sandy texture) (Leite et al. 2006a). Soils of the cerrado are, in general, deep and loamy providing excellent storage capacity of rainfall, rich in aluminum and with low pH, but deficient in nutrients (Sousa & Lobato 2004). The soil of the pasture had higher levels of aluminum and lower pH values and lower combined calcium, potassium and magnesium than the soil of the campus (Leite et al. 2006a). The *C. brasiliense* (Oliveira 1997; Leite et al. 2006a) and its Coleoptera and Lepidoptera species may have adapted to these challenging cerrado conditions (i.e., poor and acid soils). Leite et al. (2012) observed that *C. brasiliense* trees in areas where the soils contained higher levels of summed chemical bases and total sand (fine + gross) were less healthy. Moreover, the areas whose soils contained higher levels of aluminum and clay had higher percentages of healthy *C. brasiliense* trees and branches. Overall, higher mortality of *C. brasiliense* trees may be associated with higher pH and lower content of aluminum, silt and clay, with competition with other tree species for nutrients, water and light, with the attack of Cossidae (Lepidoptera) and particularly with the attack of *Phomopsis* sp. fungi. Leite et al. (2011d) had observed higher numbers of cossid pupae and more frass produced by Cossidae (Lepidoptera) in *C. brasiliense* in soils that had higher levels of potassium, calcium, magnesium, summed bases, cationic exchange capacity and organic matter and lower amounts of fine sand.

The Coleoptera and Lepidoptera species with higher potentials to become pests in commercial *C. brasiliense* plantations are *Apoptus* sp. (Coleoptera: Curculionidae) and lepidopteran miners on leaves, and *Carmenta* sp. (Lepidoptera: Sesiidae) on fruits. Besides these, *Eurytoma* sp., *A. gossypii*, and *Phomopsis* sp. on leaves, wood boring Cossidae in trunks, and *E. rufomarginata* on flowers and fruits are important pests on *C. brasiliense* (Leite et al. 2006b, 2007, 2009, 2011d, 2012).

Farmers have preserved forest or cerrado areas where the soil conditions are poor (more sandy or rocky, as noted in areas of cerrado in the north of Minas Gerais State), and where the production and natural regeneration of *C. brasiliense* is reduced (Leite et al. 2006a, 2011d, 2012). On pastures, the rate of natural regeneration by seedlings of *C. brasiliense* is also low. Although the pasture soils have more clay, the seedlings of this plant are constantly pruned by cultivation, burning, or grazing (Leite et al. 2006a). Moreover, in both pasture and cerrado, fruit collectors remove almost all fruits of *C. brasiliense* and thus reduce considerably the natural propagation of this plant. All of this can lead to a serious risk of increased insect attack and extinction of *C. brasiliense* (Leite et al. 2006a).

Greater habitat diversity and more complex plant architectures favored populations of Coleoptera and Lepidoptera and their predators. Ants, spiders, and predatory bugs are important in the reduction of these groups of herbivores. Higher wind speeds can induce defoliators to shelter on trees with wider crowns. The positive correlations of soil aluminum content and acidity with defoliators indicate that these species are adapted to the natural cerrado conditions.

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