

**Leonardo Tullio
(Organizador)**

**CARACTERÍSTICAS DOS
SOLOS E SUA INTERAÇÃO
COM AS PLANTAS**

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Leonardo Tullio
(Organizador)

Características dos Solos e sua Interação com as Plantas

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APRESENTAÇÃO

A obra “Características dos solos e sua interação com as plantas” aborda uma apresentação de 18 capítulos, no qual os autores tratam as mais recentes e inovadoras pesquisas voltadas para a área da Ciência do Solo.

O envolvimento das plantas com o solo requer conhecimento técnico de alto nível, pois a interação Solo – Planta – Ambiente é sem dúvida um universo complexo de informações e resultados que são influenciados por vários agentes externos e internos e que respondem no potencial produtivo de uma cultura. Entretanto, essa interação exige modelagem de dados que muitas vezes são inacabáveis, fazendo assim estimativas conforme os parâmetros estudados.

Porém, com a pesquisa voltada cada vez mais para o estudo do ambiente como um complexo sistema de produção, torna-se favorável para conhecer mais sobre os processos químicos, físicos e biológicos envolvidos no solo e na planta.

Assim, o conhecimento da relação Solo - Planta é fundamental para o entendimento desse sistema de produção, no qual a sua interação com as diversas características define seu potencial.

Por fim, espero que esta obra atenda a demanda por conhecimento técnico de qualidade e que novas pesquisas surjam neste contexto.

Leonardo Tullio

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EFFECTS OF SOIL, SPATIAL PARAMETERS AND FOLIAR PHENOLIC CONTENTS ON ENTOMOFAUNA VARIABILITY IN PEQUIZEIRO

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RESUMO: Variações na entomofauna das folhas de *Caryocar brasiliense* em onze populações do Cerrado central brasileiro foram analisadas utilizando-se os conteúdos de fenólicos totais, além de parâmetros edáficos e espaciais dos locais de coleta. Os insetos da ordem Coleoptera tiveram pouca ocorrência em folhas com teores elevados de fenóis e taninos totais. No entanto, esses insetos foram encontrados parasitando folhas de pequi em locais com os maiores teores de micronutrientes nos solos. Representantes das ordens Hymenoptera e Lepidoptera desenvolveram galhas em plantas com teores elevados de taninos totais e

condensados. A ordem Hemiptera apresentou distribuição homogênea, enquanto que insetos das ordens Neuroptera, Diptera e Orthoptera comportaram-se como visitantes, sem nenhum relacionamento com *C. brasiliense*, durante as observações de campo. A maioria (97,1%) da entomofauna foliar foi explicada baseando-se em dados edáficos, químicos e espaciais, como conjuntos preditores, com contribuições de 64,5%, 22,7% e 60,6% da variação total, respectivamente. A maioria da variância residual (2,9%) foi atribuída a antropização dos locais de amostragem.

PALAVRAS-CHAVE: *Caryocar brasiliense*, pequi, variabilidade química, solo degradado, insetos.

ABSTRACT: Leaf entomofauna variation in eleven *Caryocar brasiliense* populations from central Brazilian Cerrado was analyzed based on total phenolic contents, as well as edaphic and spatial parameters of the sampling sites. Insects of the order Coleoptera had low occurrence in leaves that showed high levels of total phenols and tannins. However, they were found in leaves of plants growing on soils with higher micronutrient contents. Insects of the orders Hymenoptera and Lepidoptera developed galls on plants with high levels of total and condensed tannins. Hemiptera showed a homogeneous distribution, whereas species of the orders

Neuroptera, Diptera, and Orthoptera behaved as visiting insects, without establishing any relationship with *C. brasiliense* during field observations. Approximately 97% of the entomofauna variability was explained by edaphic, chemical, and spatial data sets as predictor variables, whose contributions were 64.5%, 22.7%, and 60, 6% of the total variation, respectively. Most of the residual variance (2.9%) was attributed to the anthropization of sampling sites.

KEYWORDS: *Caryocar brasiliense*, pequi, chemical variability, soil degradation, insects.

1 | INTRODUCTION

The Cerrado biome occupies Brazil's central plateau and spans about a quarter of the country's territory. Different phytophysiognomic features, from grassland to forest formations, known by various local names, form a mosaic in the landscape (FRANCO; HARIDASAN, 2008). Despite Cerrado's status as a biodiversity hotspot which houses over 11,000 species of native plants, including 4,400 endemic species, only about 2.2% of its area enjoys legal protection (MARRIS, 2005). Central Brazilian Cerrado was severely fragmented and degraded by deforestation in the early 1950s, a process accelerated in the 1970s with the expansion of the agricultural frontier. An estimation by remote sensing shows that about 47.8% of Cerrado's original vegetation had been cleared by 2008, mainly due to cultivated pastures and agricultural crops. After the Atlantic Forest, Cerrado is the Brazilian biome that has suffered the greatest anthropogenic impacts, and it has been classified among the most threatened biomes in the world (SANO et al., 2010).

Caryocar brasiliense Camb., Caryocaraceae (pequi, pequiizeiro) is its regional symbol and predominates over other native fruit species in the Cerrado of State of Goiás. The occurrence of pequi may vary from 15 to 180 individuals per ha, playing a major role in the regional economy (VERA et al., 2005). The fruit pulp is edible after cooking and rich in vitamins, lipids, and proteins. It is used to flavour rice, with a strong presence in cooking as a substitute for oil and butter. In addition, it is used in cosmetics and in the production of soaps, creams, and sorbets. Pequi is also commonly used in traditional medicine as an antiseptic, applied to external bumps, bruises, and scarring (MENDES; CARLINI, 2007). Essential oils from its leaves and seeds have been reported to show antifungal activity against etiologic agents of human systemic mycosis (PASSOS et al., 2003; DAMIANI et al., 2009).

In State of Goiás, pequi's production is irregular; its plants suffer intense attack by insects that cause damage to trunks, flowers, fruits and leaves, limiting and compromising its production. A recent study on insect biodiversity in pequi identified 194 species of insects belonging to 72 families and 10 taxonomic orders (FERREIRA et al., 2009). These include species such as foraging ants, Hemiptera (aphids), caterpillars and insect galls. The species that attack the pequi are found on its leaves, shoots and stems,

forming galleries and scraping the fruit. Many of the insects found usually copulate and feed on the leaves, causing leaf area reduction, affecting plant photosynthesis and compromising the potential production of pequi fruits. Due to seasonal rainfall and the drought cycle in the Cerrado, insect fauna increases from September to November alongside the abundance of food. During this period, Hymenoptera, Coleoptera, Lepidoptera and Hemiptera insects are dominant, showing the highest rates in the Cerrado fauna, which coincides with pequi's flowering and ripening (SILVA; FRIZZAS; OLIVEIRA, 2011). Despite the entomofauna distribution of pequi has been described (LEITE et al., 2012; NEVES et al., 2012), it was related to different habitats or seasonal influences, and to our knowledge, no plant secondary metabolites and soil nutrient effects on insect variability have been reported for this tree yet.

Several studies have shown that the environment may have direct and indirect effects on insect assemblies. For example, phenol production and accumulation is one of the strategies involved in plant defense systems on biotic stress factors, such as herbivory or microbial infection. Soil characteristics, habitat types and management regimes also strongly influence invertebrate communities (LENARDIS et al., 2007).

In this study, chemical variability in total phenols, flavonoids and tannins of pequi leaves, as well as soil physicochemical characteristics and anthropization level of sampling sites were assessed to differentiate eleven populations of pequi from State of Goiás according to entomofauna distribution. Local and spatial insect variability patterns and factors associated with this variation may provide important information for insect control, management and adoption of conservation measures for pequi, as well as for better exploitation of this native Cerrado plant.

2 | MATERIAL AND METHODS

2.1 Plant material

Leaf collection was performed from August 2004 to December 2006, in eleven pequi populations in State of Goiás in sampling sites exhibiting different soil degradation levels (Table 1).

	Site	Latitude (S)	Longitude (W)	Altitude (m)	Declivity (%)	Anthropization degree
1	Morrinhos	17° 37' 51"	48° 48' 19"	683	9.0	total
2	Hidrolândia	16° 57' 35"	49°10' 53"	768	6.0	total
3	Paraúna	16° 50' 26"	50°38' 44"	725	6.0	median
4	Iporá	16° 25' 55"	51°02' 14"	497	3.0	total
5	Faina	15° 28' 44"	50°24' 11"	393	5.0	total
6	Araguapaz	15° 17' 58"	50°26' 27"	328	3.0	high
7	Mutunópolis	13° 37' 49"	49°13' 32"	382	4.0	very low
8	Formoso	13° 39' 36"	48°48' 37"	415	8.0	low
9	Alvorada do Norte	14° 30' 57"	46°34' 24"	517	1.0	low

10	Damianópolis	14° 34' 48"	46°12' 29"	780	2.0	low
11	Mambaí	14° 32' 05"	46°05' 36"	680	1.5	high

Table 1. Pequi collection with the location of populations in State of Goiás, Brazil

In each site, leaf samples were collected from plants found in the reproductive stage (with flowers or fruits). Leaves were collected from the four geographic quadrants of the canopy of at least four nearby trees, composing a single sample, which was repeated at least three times resulting in a total of 41 samples. The soil was also collected at a 0-20 cm depth in each population. A total of 17 physicochemical parameters were analyzed. The pH was determined in a 1:1 soil-water volume ratio. Ca^{2+} , Mg^{2+} and Al^{3+} were extracted with 1 mol L^{-1} KCl, and P, K^+ , Zn^{2+} , Cu^{2+} , Fe^{2+} , Mn^{2+} were extracted with Mehlich's solution. Concentrations of K^+ , Ca^{2+} , Mg^{2+} , Cu^{2+} , Fe^{2+} , Mn^{2+} , and Zn^{2+} were measured by flame atomic absorption spectrometry (AAS, Perkin Elmer), phosphorous was determined by spectrophotometry (DU-70 Spectrophotometer, Beckmann). Organic matter (OM), cationic exchange capacity (CEC), potential acidity ($\text{H}^+ + \text{Al}^{3+}$), Al^{3+} , and soil texture were determined by applying the usual methods.

2.2 Plant extracts and metabolite quantifications

Leaves from each sampling site, previously dried at 29°C for 7 days and powdered (30 mesh), were twice subjected to total phenol extraction with ethanol-water (1:1) in the ultrasonic bath for 30 min. The extract was centrifuged at 4000 rpm (10 min) and the supernatant was transferred to a 25 mL volumetric flask. The extraction process was conducted in duplicate for each sample. Total phenols, flavonoids, total tannins, in addition to hydrolysable and condensed tannins were quantified according to techniques described in Pereira et al. (2017).

2.3 Statistical analyses

Analysis of variance (ANOVA) with populations as factor and Tukey as *post hoc* test was used to assess the average multiple comparisons. *p*-Values < 0.05 were considered significant. Analyses were performed in SAS using GLM procedure. Canonical correspondence analysis (CCA) was used to examine the relationship between the matrix of presence/absence insect species in the leaves (41 samples × 95 variables), representing a response matrix conditioned by soil (41 × 17; edaphic matrix) and foliar phenolic contents (41 × 5; chemical matrix), defined as environmental explanatory variables. CCA was performed in Canoco (LEPŠ; ŠMILAUER, 2012).

Significant soil variables (Cu^{2+} , Zn^{2+} , Mn^{2+} , Al^{3+} , P, and silt) and leaf phenolic contents (total phenols, flavonoids, tannins, and hydrolysable tannins) were selected by forward stepwise selection using variable inflation factor ($\text{VIF} < 5$) as criteria for assessing multicollinearity in regressions. Subsequently, discriminant analysis (DA) was applied for the validation of natural sample clusters based on the first CCA's factorial

plane. Total variation partitioning (inertia) was performed with the response data and the chemical, edaphic, and spatial matrices as explanatory data sets using partial CCAs (pCCAs). Initially, the spatial matrix consisted of the two geographical coordinates of the Universal Transverse Mercator (UTM) system, altitude, and declivity of sampling sites, which were summarized for the first two axes of a principal component analysis (PCA). These new coordinates (x and y) were supplemented to the terms of a third-degree polynomial, which summarized linear trends (x , y , xy) and complex surfaces that require the quadratic (x^2 , y^2 , x^2y , xy^2) and cubic (x^3 , y^3) terms. After stepwise selection with VIF adjustments, significant monomials (x , yx^2 , xy , y^3 , y^2 , x^2) represented the final spatial matrix (41'6). The effect of anthropization on the entomofauna was subsequently obtained by the pCCAs of total inertia's first partitioning. Prior to the multivariate analyses, phenolic contents were transformed by $\log(x)$; soil macro and micronutrients by $\log(x+2)$, whereas organic matter, and texture underwent angular transformation. In addition, the entomofauna was downweighed to avoid the influence of rare insect species.

3 | RESULTS AND DISCUSSION

The insects collected in pequi leaves totaled 95 species distributed in seven taxonomic orders. From these, 39 were identified to the genus level. Coleoptera showed the largest number of representatives (39%), followed by Hemiptera (27%), Hymenoptera (12.6%), Lepidoptera (9.4%), Orthoptera (6.2%), Diptera (3%), and Neuroptera (1.8%). However, when considering the insect fauna present in the whole plant, the order Hemiptera showed the highest (25.6%) species richness (FERREIRA et al., 2009). In a previous study (LEITE et al., 2012), the entomofauna of pequi from the State of Minas Gerais included insects belonging to Coleoptera and Hemiptera also showing the highest species richness (*ca.* 53%).

The texture of soil sampling sites showed clay (11-41%), silt (1-13%) and sand (46-78%) contents (Table 2), which confirm pequi's high plasticity.

Parameter	Soil sampling sites										
	1	2	3	4	5	6	7	8	9	10	11
Clay ^a	37	34	11	24	24	27	37	30	17	14	14
Sand ^a	50	55	87	70	58	64	50	66	82	85	82
Silt ^a	13	11	2.0	6.0	8.0	9.0	13	4.0	1.0	1.0	4.0
pH	5.4	4.8	4.2	4.1	5.0	4.4	4.1	4.9	4.2	4.1	4.3
OM ^{a,d}	1.6	1.9	1.3	0.9	2.7	1.4	1.2	1.4	0.4	0.3	0.2
P ^b	2.3	2.7	2.3	1.8	4.7	3.7	2.3	2.3	8.2	3.2	2.3
K ^{+,b}	161	164	36	40	112	71	65	107	28	16	29
Cu ^{2+,b}	1.4	1.2	0.2	0.4	0.2	1.0	1.1	1.2	0.4	0.2	0.2
Fe ^{3+,b}	95.7	68.2	54.1	84.1	42.6	106.3	102.4	46.9	49.1	46.9	32.2
Mn ^{2+,b}	25.6	37.6	42.6	13.9	64.8	39	25.6	150.7	8.3	8.2	34.1
Zn ^{2+,b}	1.1	0.5	0.4	0.3	1.6	0.7	0.5	1.7	0.2	0.4	0.4

Ca ²⁺ ,c	2.7	1.8	0.2	0.9	2.8	1.6	0.8	1.7	0.9	0.2	0.7
Mg ²⁺ ,c	1.4	0.7	0.1	0.3	0.9	0.6	0.3	0.7	0.3	0.1	0.5
CEC ^{c,e}	7.0	6.8	2.9	5.6	7.1	5.9	5.6	6.6	4.4	3.1	4.4
H ⁺ +Al ³⁺ ,c	2.5	3.9	2.5	4.3	3.1	3.5	4.3	3.9	3.1	2.8	3.1
Al ³⁺ ,c	0.0	0.4	1.3	2.4	0.0	1.0	2.1	0.1	1.4	1.8	1.7

Table 2. Texture and physicochemical parameters of soil sampling sites

^a(%); ^b(mg L⁻¹); ^c(cmol_c L⁻¹); ^dOM = organic matter; ^eCEC = cationic exchange capacity; site codes (1-11): see **Table 1**.

These results agree with the wide distribution range in terms of soil quality and nutrient availability observed for *C. brasiliensis*. Soil pH was considered appropriate only in the Morrinhos (1) and Faina (5) populations. In most sites it was considered low and strongly acid (pH 4.1-4.9), a finding consistent with previous studies that indicate high acidity in the Cerrado soil (VERA et al., 2005). In general, soil samples showed low nutrient levels for plants, such as those of Ca²⁺ (0.2-2.8 cmol_c L⁻¹), P (1.8-8.2 mg L⁻¹) Mg²⁺ (0.1-1.4 cmol_c L⁻¹) and K⁺ (16-164 mg L⁻¹).

Total phenolic contents of pequi leaves are presented in Table 3. ANOVA results reveal broad variation in hydrolysable tannin contents (85.0 to 135.4 mg g⁻¹), with the lowest value found in the Damianópolis (10) samples. This sampled area also showed the lowest tannin contents in leaves (90.6 mg g⁻¹).

Site	Phenols	Flavonoids	Tannins	Condensed tannins	Hydrolyzable tannins
1	146.4 b	10.5 ab	96.6 ab	2.3 a	89.9 d
2	146.1 b	10.3 ab	108.8 ab	2.4 a	111.5 bcde
3	181.8 ab	12.3 ab	104.8 ab	3.4 a	100.1 cde
4	186.3 ab	13.4 ab	104.2 ab	2.6 a	106.9 bcde
5	201.6 ab	11.8 ab	127.8 a	2.5 a	135.4 a
6	202.7 ab	8.2 b	116.8 ab	2.5 a	117.7 abcd
7	189.1 ab	10.3 ab	130.9 a	2.8 a	127.9 ab
8	210.4 ab	11.7 ab	117.8 ab	2.3 a	126.3 abc
9	217.5 a	11.2 b	122.4 ab	2.3 a	132.4 ab
10	187.4 ab	15.5 a	90.6 b	2.7 a	85.0 e
11	188.5 ab	14.1 a	118.6 ab	2.5 a	113.6 abcd

Table 3. Phenolic contents (mg g⁻¹) of pequi leaves collected from eleven populations

Averages followed by small letters in the column did not share significant differences at 5% probability by Tukey's test; site codes (1-11): see **Table 1**.

Total phenols showed high levels in most samples (181.8 to 217.5 mg g⁻¹), except in the Morrinhos (1) and Hidrolândia (2) sites (mean 146.3 mg g⁻¹). Flavonoids showed the highest mean contents (14.8 mg g⁻¹) in the northeastern region of State of Goiás (Damianópolis (10) and Mambaí (11)), whereas no significant differences were obtained

in condensed tannins from leaves of different sampling sites.

As regards phenolic distribution, significant amounts were obtained in most samples, which showed low soil fertility. This finding may be accounted by the fact that phenolics were protecting leaves by acting as antioxidants. Thus, a higher concentration was required to protect leaves from abiotic stresses (INGERSOLL et al., 2010). Other studies on phenolic variation in Cerrado plant species have suggested that edaphic factors could strongly affect the amounts of phenolic contents in leaves (SANTOS et al., 2011). In this study, phenolic variations could also be related to leaf growth and development as well as to herbivore pressure. During leaf collecting, there were several flushes of new leaves in different populations, which coincide with the proliferation of insects. These two factors also have been important for influencing phenol variation in plants (SOLAR et al., 2006) such as *Quercus robur* L. (Fagaceae) and *Juglans regia* L. (Juglandaceae). Additionally, leaves under herbivore attack have shown an increase in the level of endogenous defenses, such as hydrolysable tannins (BARBEHENN et al., 2009).

CCA results show a strong correlation ($R = 0.976$) and 71.2% of variance in entomofauna can be explained by environmental variables. This variation fraction, ca. 41%, was retained in the first CCA's plane (Figure 1). Permutation test on the first two CCA axes and on the sum of the axes indicates that the data structure is highly significant ($p < 0.001$) i.e. not due to random effects.

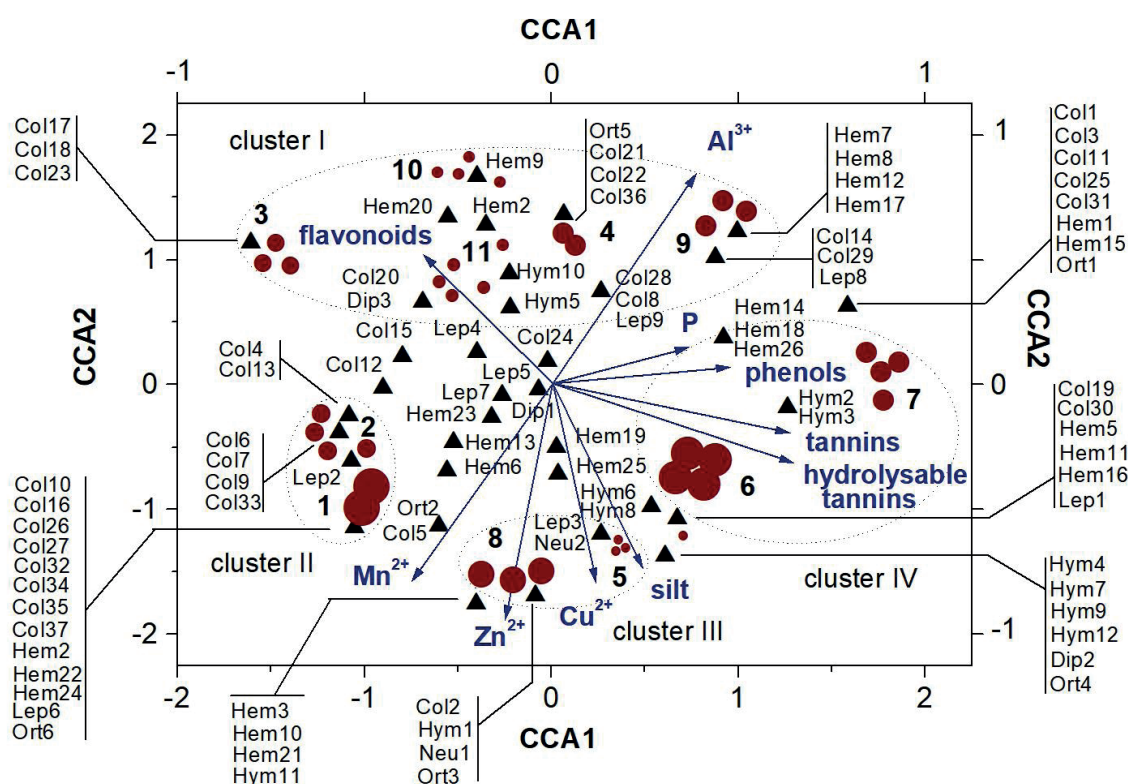


Figure 1. CCA triplot showing the leaf entomofauna (▲) of pequi samples (●), with the size corresponding to insect richness. Significant soil and foliar parameters are represented by vectors from the origin. Fitted variables (insects) whose values were $< 20\%$ are not shown: Col = Coleoptera; Hem = Hemiptera; Hym = Hymenoptera; Lep = Lepidoptera; Dip = Diptera; Neu = Neuroptera; Ort = Orthoptera. Site codes (1-11): see Table 1.

In Figure 1, an increase in the value of CCA1 (22.6% of total inertia) was associated mainly with an increase in total phenols, tannins and hydrolyzed tannins, as well as with decrease in flavonoid contents. On the other hand, an increase in the value of CCA2 (18.4% of the total inertia) was highly correlated with a decrease in soil micronutrients. Therefore, CCA1 mainly describes variability in foliar phenolics, whereas CCA2 is related to the soil fertility gradient of the sampling sites. CCA results also suggested greater insect richness in pequi populations located in soils rich in micronutrients (populations **1**, **2**, **6**, **7** and **8**). On the other hand, high phenolic content was correlated to greater insect richness of orders Hymenoptera and Hemiptera (populations **6** and **7**), whereas lower values of these chemical groups have been mainly related to Coleopteran insects (populations **1** and **2**).

Tannins and hydrolysable tannins revealed moderate relationships with Cu^{2+} and Zn^{2+} , while total phenols and flavonoid contents increased with the deficiencies of these micronutrients, mainly Cu^{2+} , and Mn^{2+} . Several works have reported the involvement of Cu^{2+} and Mn^{2+} in the shikimic acid pathway leading to the biosynthesis of phenolics (LIN; CHENG; LUI, 2005; GUANGQIU; CHONGLING; HAOLIANG, 2007). In plants with Cu^{2+} and Mn^{2+} deficiency lignification is impaired and phenolics accumulate in the plant tissues. A dose response effect of Cu^{2+} on foliar condensed tannins in seedlings of *Aegiceras corniculatum* (L.) Blanco (Myrcinaceae) had been observed. At first tannins decreased with an increase in Cu^{2+} supply; however, when Cu^{2+} reached toxic levels the tannin concentration also increased. These results have shown that the biosynthesis of phenolics is dependent on Cu^{2+} and Mn^{2+} levels: in deficient tissues lignification is inhibited, then so the production of other phenolics is enhanced. When Cu^{2+} and Mn^{2+} achieve sufficient levels lignin biosynthesis increases, most likely using other phenolics as intermediates. The same negative trend in Zn^{2+} /flavonoids relationship also were described in *Citrus* leaves, whose flavonoid content increased with zinc-deficiency (MANTHEY et al., 2000). On the other hand, the flavonoid increase in very poor soil (populations **3**, **4** and **9-11**) may be attributed to a stress-type promotion as a response to Al^{3+} (FEUCHT et al., 1999).

Phytophagous insects belonging to the order Hemiptera presented a more homogeneous geographical distribution between sample collections, except in Paraúna (**3**), which showed an absence of insects from this order. This distribution suggests that both soil nutrients and foliar phenolic contents have little bearing on the dispersal of Hemiptera in pequi, a similar behaviour to that of generalist insects. This may also explain, at least partially, the predominance of this insect order in the entomofauna of *C. brasiliensis* from different Cerrado phytophysionomies (LEITE et al., 2012).

On the other hand, the order Hymenoptera showed galling insects associated with pequi from Araguapaz (**6**), especially in Eurytomidae (present in all sampled sites), Eulophidae and Torymidae. These insects have shown high specialization in plant community structure and have been characterized by their high incidence in plants that accumulate phenols and tannins (GONÇALVES-ALVIM; FERNANDES, 2001). Thus,

high tannin concentration in the galls could favour the survival of galling insects as it decreases the effectiveness of natural enemy attacks and the proliferation of fungi that can eliminate the gall (SCARELI-SANTOS; VARANDA, 2009). Similar results were observed in *Aspidosperma spruceanum* Benth. ex Müll. Arg. (Apocynaceae), on which the presence of Cecidomyiidae (Diptera) gall insects occurred during periods of the highest phenol concentration, suggesting that this chemical barrier could favour the protection of these insects (FORMIGA et al., 2009).

Ant species (*Cephalotes* spp. and *P. clavata*) were mainly found in Araguapaz (6) and showed preference for leaves with higher tannin content. A similar preference was observed for *Atta cephalotes*. The ability of ants' resistance to tannins may be associated with fungi cultivated by these insects, which are capable of polymerizing and inactivating the phenolics. According to Nichols-Orians (1991), the pattern in the distribution of *A. cephalotes* in plants is dependent on the amount of condensed tannins induced by solar stress (12.8 mg proanthocyanidin per gram of dry leaves). In the present work, condensed tannins (2.6 ± 0.3 mg of proanthocyanidins per gram of dry leaves) did not show any significant differences, thus suggesting the same magnitude in solar stress over *C. brasiliense* sampling sites.

In our field work, the ants were observed removing caterpillars, which can be partly responsible for the trend observed in these insect's distribution. In pequi, ants significantly reduced the infestation levels by the caterpillars, as *Eunica bechina*, especially in the vicinity of extrafloral nectars and establishing a defense mutualism (OLIVEIRA, 1997; ROSUMEK et al., 2009). Field study has shown that visiting ants can act as anti-herbivore agents and reduce leaf damage on trees of *Qualea grandiflora* Mart. (Vochysiaceae) or may affect herbivorous fauna and masked the expected effects of tannin on herbivore richness and abundance in *Copaifera langsdorffii* Derf. (Caesalpiniaceae) leaves (COSTA et al., 2011).

Insects belonging to the orders Neuroptera, Diptera and Orthoptera were considered visitors (11% of entomofauna), without establishing any relationship with the plant during data collection (FERREIRA; VELOSO, 2009). The CCA triplot shows that these insects had higher selectivity for soils with higher micronutrient contents. Insects of the order Coleoptera showed a higher incidence in regions with the lowest levels of total and hydrolysable tannins, as well as in soils with higher micronutrients and lower aluminum contents. Morrinhos (1) and Hidrolândia (2) presented the highest number of beetles, and a reduction of pequi leaves caused by herbivory. Insects of this order show an association with the pequi, mating and feeding on its leaves (SILVA et al., 2011). Experiments conducted with *Clitoria fairchildian* R. A. Howard (Fabaceae) revealed that the tannins are relevant for inhibition and development of wood beetles in *C. fairchildian* trunks with higher tannin levels (LUNZ et al., 2007).

Chewing insects belonging to the orders Lepidoptera, Hymenoptera and Coleoptera showed a higher density at the bottom of the CCA triplot and strong correlations with Mn^{2+} and Zn^{2+} from soil sampling sites. These results agree with the factors involved

in jaw features. Jaws are extremely resistant to abrasion due to the incorporation of metals such as Zn^{2+} and Mn^{2+} in their cuticular cutting matrix. Up to 5% of Zn^{2+} was recorded in some jaws (RESH; CARDE, 2009). Insect larvae accumulate high concentrations of Cu^{2+} and Zn^{2+} , which are important micronutrients involved in various physiological insect processes. It has also been suggested that some metalloproteins, such as metallothionein, play important roles in the accumulation and storage of Cu^{2+} and Zn^{2+} in insects (PING; HUILING; WENSHENG, 2009).

The CCA triplot suggested four sample clusters, two of which (clusters III and IV) along the São Patrício Valley. These clusters were validated by discriminant analysis (DA) having hydrolysable tannins, flavonoids, Cu^{2+} , and Al^{3+} contents as predictor variables. In cluster III, Faina (5) and Formoso (8) reveals a more rugged relief with high amounts of Zn^{2+} and Cu^{2+} , whereas cluster IV (Araguapaz, 6, and Mutunópolis, 7) presents a slightly rough relief and acidic and nutrient-poor soils with high Al^{3+} contents. The anthropization degree was higher in 7 and Formoso (8) and considered lower for 5 and 6. On the other hand, Morrinhos (1) and Hidrolândia (2) (cluster II) were discriminated by moderated flavonoid contents. This sample collection was located near the highway BR-153, which may have favoured the spread of Coleoptera insects. Cluster I with samples from Paraúna (3), Iporá (4), Mutunópolis (7) and Mambaí (11) was characterized by low levels of soil micronutrients and the highest content of Al^{3+} and flavonoids. This group showed a lower incidence of insects when compared to the other clusters. Even though flavonoids contribute to plant resistance to insects (SIMMONDS, 2003), the limited availability of soil nutrients and low human disturbance at these sites may influence the behaviour of insect herbivores. In fact, pequi trees located in preserved Cerrado had lower richness and abundance of insect herbivores than those in pastureland or *Eucalyptus* plantations (NEVES et al., 2012).

The above results indicated that the entomofauna community in pequi leaves is at least partially controlled by chemical signals, which depend on plant-soil interactions. Similar results were reported for wheat and coriander, whose arthropods assemblies were ordered in relation to the volatile organic compounds (VOCs) emitted by crops (LENARDIS et al., 2007). Although a low percentage of the variance was explained by edaphic properties, soil micronutrients appeared as the main factors structuring the data. Other studies have shown the importance of the soil fertility management to induce change in crop insect assemblies (PERNER et al., 2005).

To quantify the influence of each environmental data set, the foliar entomofauna was submitted to variation partitioning through pCCAs. Variation partitioning decomposes the canonical variance (inertia) into canonical axes for each analysis, which can be tested on their statistical significance by the Monte Carlo permutation test. All fraction of variations was significant ($p < 0.03$) and the results are visualized by Venn diagram (Figure 2).

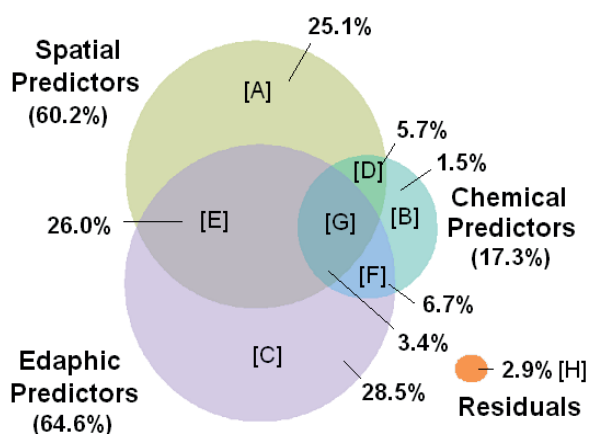


Figure 2. Venn diagram of variation partitioning of *C. brasiliense* entomofauna by partial CCAs.

Predictors: spatial data consisted of significant monomials (x , yx^2 , xy , y^3 , y^2 , x^2) of polynomial trend surface originated from the first two PCA axes of UTM coordinates, altitude and declivity of sampling sites. Soil data consisted of significant parameters (Cu^{2+} , Zn^{2+} , Mn^{2+} , Al^{3+} , P, and silt) and chemical data of foliar phenolic contents.

Results show that 97.1% of total variation in the entomofauna data set ([A-G]) may be explained by predictor matrices, resulting in a model whose residue was 2.9% ([H]). It was observed that 72% of the insect's variability can be explained by soil characteristics and foliar phenolic contents ([B-G]). Although foliar phenolics offer a small pure contribution ([B] = 1.5%), it was significant ($p < 0.03$). On the other hand, incorporating the joint effects of foliar chemical contribution explained 17.3% ([B+D+F+G]) of the entomofauna variance in pequi leaves. The largest total contribution in explaining insect variability was given by edaphic parameters ([C+E+F+G] = 64.6%), with spatial factors explaining a quarter of the total inertia ([A] = 25.1%). Variation partitioning has been used to assess the contribution of edaphic and spatial factors associated with essential oils and phenolic contents of plants (DUARTE et al., 2012). Similarly to the work referred previously, the phenolic contents also showed greater influence of edaphic factors.

A difficulty in assessing the anthropogenic impacts on a biological community is to differentiate anthropogenic factors from responses to natural variations in environmental conditions. Theoretical models have been proposed to predict species' responses to anthropogenic influence along stressor gradients (MORRISEY et al., 2003). However, many studies have been based on species' responses to a single environmental or biological factor (POSTHUMA; SUTER; TRAAS, 2002). In the current study, the multivariate partitioning methodology was also applied to assess the human disturbance in the entomofauna variation of pequi (Table 4).

Effects and variables	Covariables	Variation fraction	Explained variation (%)	P^a
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Total effect				
Soil-chemical-spatial, anthropization		[A+B+C]	99.97	0.001
Partial effects				
Anthropization	Soil-chemical-spatial	[A]	2.83	0.001
Soil-chemical-spatial	Anthropization	[C]	89.36	0.001
Joint effects				
Soil-chemical-spatial, anthropization		[B]	7.78	
Residuals		[D]	0.03	

Table 4. Anthropization influence in *C. brasiliense* entomofauna by partial CCAs

^aprobability on Monte Carlo permutation test (999 permutations); anthropization is represented by two levels (low and high). Spatial data consists of significant monomials (x , yx^2 , xy , y^3 , y^2 , x^2) of polynomial trend surface originated from the first two PCA axes of UTM coordinates, altitude and declivity of sampling sites. Soil data consisted of significant parameters (Cu^{2+} , Zn^{2+} , Mn^{2+} , Al^{3+} , P, and silt) and chemical data of foliar phenolic contents.

The results showed that the anthropization degree accounts for 10.6% ([A+B]) of total insect variation. This finding is consistent with those that associate the highest occurrence and insect diversity of the Coleoptera order with the highest degree of disturbance of the integrity of the natural environment (LEITE et al., 2012; FAVERO; SOUZA; OLIVEIRA, 2011). Thus, the entomofauna of pequi could reflect specific environmental factors, its insect composition being influenced by soil parameters and foliar phenolic contents.

4 | CONCLUSION

The experimental approach used in this study allowed for the separation of the effects of soil nutrients and anthropization levels in sampling sites, and foliar phenolic contents on the entomofauna diversity of pequi leaves. Soil micronutrients, e.g. Mn^{2+} , Zn^{2+} , Cu^{2+} and Al^{3+} , and foliar phenolic contents, particularly total phenols, tannins and hydrolysable tannins could be involved in insect assemblies. Based on these results, the entomofauna on *C. brasiliense* are, at least, partially controlled by chemical signals, which depended on plant-soil interactions. However, other factors, such as interspecific competition, predation, and parasitism may act together to shape the patterns of insect distribution. The results of this work provide a platform from which we can further pursue our understanding of chemical defenses in Cerrado plant species in relation to herbivory.

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