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Original Article

Changes in galling insect community on *Caryocar brasiliense* trees mediated by soil chemical and physical attributes

Mudanças na comunidade de insetos galhadores em plantas de *Caryocar brasiliense* mediadas por atributos químicos e físicos do solo

G. L. D. Leite[a], R. V. S. Veloso[b*], M. A. Soares[b], L. F. Silva[a], P. F. S. Guanãbens[c], E. J. M. Munhoz[d], W. R. Pereira[a], R. S. Silva[b], G. W. Fernandes[e] and J. C. Zanuncio[f]

[a]Universidade Federal de Minas Gerais, Instituto de Ciências Agrárias, Insetário George Washington Gomez de Moraes, Montes Claros, MG, Brasil

[b]Universidade Federal dos Vales do Jequitinhonha e Mucuri, Departamento de Agronomia, Diamantina, MG, Brasil

[c]Instituto Federal de Educação Ciência e Tecnologia de Minas Gerais, São João Evangelista, MG, Brasil

[d]Universidade Federal do Espírito Santo, Divisão de Meio Ambiente e Sustentabilidade, Vitória, ES, Brasil

[e]Universidade Federal de Minas Gerais, Departamento de Genética, Ecologia & Evolução, Belo Horizonte, MG, Brasil

[f]Universidade Federal de Viçosa, Instituto de Biotecnologia Aplicada à Agropecuária, Departamento de Entomologia, Viçosa, MG, Brasil

Abstract

The nutrient stress hypothesis predicts that galling insects prevail on host plants growing in habitats with soils of low nutritional quality. *Caryocar brasiliense* (Caryocaraceae) is host to four different leaf-galling insects. These insects have the potential to cause a reduction in the production of *C. brasiliense* fruits, an important source of income for many communities in Brazil. We studied the effects of soil physical and chemical characteristics on the abundance, species richness, and diversity of galling insects and their natural enemies on *C. brasiliense* trees growing under three different soil conditions. Our data corroborate the hypothesis that in nutritionally poor (e.g., lower phosphorus content) and worse physical textures (e.g., sandy) soils, host plants support higher species richness and diversity of galling insects. However, the abundance of *Eurytoma* sp. (the most common gall in *C. brasiliense*), was correlated with a higher phosphorus concentration in the soil (better nutritional condition). The percentage of galled leaflets and the area of leaflets occupied by *Eurytoma* sp galls were higher in the more fertile soil. In this soil, there was greater abundance, species richness, and diversity of parasitoids of *Eurytoma* sp. (e.g., *Sycophila* sp.) and predators (e.g., *Zelus armillatus*). Our data indicate the importance of habitat quality in the composition of the galling insect community and the impact of soil properties in mediating the distribution of these insects in *C. brasiliense*.

Keywords: *Eurytoma* sp., pequi, plant stress, predators, *Sycophila* sp.

Resumo

A hipótese de estresse nutricional prevê que insetos galhadores prevalecem em plantas hospedeiras que crescem em habitats com solos de baixa qualidade nutricional. *Caryocar brasiliense* (Caryocaraceae) é hospedeiro de quatro diferentes espécies de insetos galhadores. Estes insetos têm potencial para afetar a produção dos frutos de *C. brasiliense*, uma importante fonte de renda para muitas comunidades no Brasil. Neste trabalho, estudamos os efeitos das características físicas e químicas do solo sobre a abundância, riqueza e diversidade de espécies de insetos galhadores e seus inimigos naturais. O estudo foi realizado em plantas de *C. brasiliense* em três diferentes condições de solo. Nossos dados corroboram a hipótese de que, em solos nutricionalmente pobres (por exemplo, menor teor de fósforo) e de texturas físicas piores (por exemplo, arenoso) as plantas hospedeiras suportam maior riqueza e diversidade de espécies de insetos galhadores. No entanto, a abundância de *Eurytoma* sp. (galhador mais comum em *C. brasiliense*), foi correlacionada com maior concentração de fósforo no solo (melhor condição nutricional). A porcentagem de folíolos da planta hospedeira galhada e a área de folíolos ocupada por galhas de *Eurytoma* sp foi maior no solo mais fértil. Neste solo, houve maior abundância, riqueza de espécies e diversidade de parasitóides de *Eurytoma* sp. (por exemplo, *Sycophila* sp.) e predadores (por exemplo, *Zelus armillatus*). Nossos dados indicam a importância da qualidade do habitat na composição da comunidade de insetos galhadores e o impacto das propriedades do solo na mediação da distribuição desses insetos em *C. brasiliense*.

Palavras-chave: *Eurytoma* sp., pequi, estresse de plantas, predadores, *Sycophila* sp.

*e-mail: ronniesvelso@gmail.com
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1. Introduction

Two contradictory hypotheses try to explain the interaction between herbivorous insects and plants. The plant stress hypothesis states that herbivorous insects prefer and perform better in stressed plants (less vigorous growing plants) (Mattson and Haack, 1987; Waring and Price, 1990). On the other hand, the plant vigor hypothesis attributes a positive response of herbivores to more vigorous plants (Price, 1991). In both assumptions, the edaphoclimatic conditions, particularly nutrient and water available in the soil, determine the plant's physiological state, and ultimately the level of plant-insect interactions (Ågren and Weih, 2020; Gong et al., 2020; Velikova et al., 2020). Although analytical methods can easily determine the nutrients in the plant and soil, the trade-off between nutrients level in the soil-plant system and the host choice by galling insects are less clear and remain largely undetermined.

Caryocar brasiliense Camb. (Caryocaraceae) trees have a wide distribution in the Brazilian savanna (Cerrado) and can reach over 10 m high and 6 m of canopy width (Bridgewater et al., 2004; Leite et al., 2006). The fruits produced by *C. brasiliense* are used by humans as food, cosmetics, lubricant production, and in the pharmaceutical industry (Ferreira and Junqueira, 2007; Garcia et al., 2007; Guedes et al., 2017). This species is the main income source of many communities (Khouri et al., 2007; Pinto et al., 2016). *Caryocar brasiliense* is protected by federal laws in Brazil and are left in deforested areas of the Cerrado.

Field observations have indicated large attacks by herbivorous insects on some *C. brasiliensis* plants, with a high abundance of galling insects. Isolated *C. brasiliense* in the agro-landscape are subjected to higher leaf, flower, and fruit damage by herbivorous insects, including galling insects (Leite, 2014; Leite et al., 2022a, b; Demolin-Leite, 2024). Galling insects are the most sophisticated herbivores because they evolved the ability to modify the tissues of their host plants to produce highly specialized structures (Shorthouse et al., 2005; Tooker and Giron, 2020). In the galls induced by insects, their larvae develop away from the harsh environment while and feed on a rich food source (Price et al., 1987; Fernandes and Price, 1988).

Galling insects are extremely abundant in nature, found in all major ecosystems in the world, with many species attacking plant species of economic importance (Fernandes, 1987; Espírito-Santo et al., 2007; Araújo et al., 2013). Galling insects are not evenly distributed throughout all habitat types or regions in the world. Studies around the globe showed that they are most species rich in ecosystems where habitat harshness prevail, such as the Mediterranean-type ecosystems and Savannas, and at the canopy of rainforests, where climate resembles that of harsh environments (Fernandes and Price, 1988; Ribeiro and Basset, 2007). At a more local scale, they are influenced by habitat conditions, being more species rich and abundant in harsher habitats with soils of low nutritional quality and longer water drought periods (Fernandes and Price, 1992). Many studies throughout the world tested the habitat stress hypothesis (Fernandes and Price, 1988) and provided support to it (Bertness and Callaway, 1994; Gonçalves-Alvim and Fernandes, 2001; Cuevas-Reyes et al., 2003; Cuevas-Reyes et al., 2014; Ramos et al., 2019). Another important mechanism reinforcing the trends in galling species distribution is the pressure caused by natural enemies. Fernandes and Price (1992) showed that mortality rates caused by natural enemies, primarily parasites and predators, are higher in habitats were better environmental conditions prevail, reinforcing the habitat stress hypothesis. In spite of the many studies addressing the factors driving galling community and population trends, long-term and host traits mediated by habitat interactions represent important aspects to be further evaluated (Price and Hunter, 2005; Mendonça Junior et al., 2010; Menezes et al., 2020).

The galling insects are the most common herbivore in *C. brasiliense* plants (Leite et al., 2017). The gall-inducing insects belong to a group of specialist herbivores that feed endophytically (Tooker and Giron, 2020). Therefore, the locally available nutritional quality of the host plant plays an important role in the life history of this group. The nutritional quality of the host plant determines the oviposition preference of specialist species (Masselière et al., 2017). Gravid females of *Glycaspis* (*Synglycaspis*) (Hemiptera: Aphalaridae) choose the oviposition site according to the level of sitosterol and other sterols in the leaves of *Eucalyptus macrorhyncha* (Myrtaceae) (Sharma et al., 2016). Additionally, according to a meta-analysis study conducted by Cornelissen et al. (2008), galling insects were more abundant in vigorous plants.

In this study, we tested the habitat stress hypothesis effects on a community of galling insects mediated by soil quality (Fernandes and Price, 1988). We evaluated the abundance, species richness and diversity galling insects, the size of their galls and natural enemies on *C. brasiliense* trees growing in three distinct habitats present different soils attributes: i) sandy, ii) average texture, and iii) clayey. These habitats presented different concentrations of minerals (e.g., phosphorus), capacity of cationic exchange, among other chemical characteristics. In addition, we also tested the natural enemies hypothesis that predicts that parasitism on galls would offer represent an important pressure shaping the distribution galling insects on this host plant species (Fernandes and Price, 1992). Overall, we expect that higher diversity of galling insects would be found on hosts inhabiting the worse kinds of soils while parasites would prevail in hosts inhabiting better soil conditions.

2. Materials and Methods

2.1. Study sites

This study was performed in the municipality of Montes Claros, in the state of Minas Gerais, Brazil, for 3 consecutive years (Jun 2008 through Jun 2011). The region has dry winters and rainy summers and is classified as climate Aw: tropical savanna according to Köppen (Alvares et al., 2013). The study was performed in 3 distinct environments: 1) *strict sense* Cerrado (S 16º44'55.6" W 43º55'7.3"at 943m a.s.l. elevation with dystrophic yellow-red oxisol soil with sandy texture); 2) pasture formerly with Cerrado vegetation (S 16º46'16.1" W 43º57'31.4", at 940m a.s.l. with red dystrophic yellow oxisol soil with loamy texture), and 3) urban area in the *Campus* of the "Instituto de Ciências Agrárias da Universidade Federal de Minas Gerais (ICA/UFMG)" (S 16º40'54.5" W 43º50' 26.8"], at 633 m a.s.l. with dystrophic red oxisol with medium texture) (Leite et al., 2006). Soils with lowest nutritional quality given by physical and chemical characteristics are those of the Cerrado and the urban area; while the relatively better soil types are found in the pasture, details of these physical and chemical characteristics (Leite et al., 2006). Permission to collect in these locations/activities was granted by the landowner (UFMG). The collected arthropods are not endangered and do not represent protected species.

A typical Cerrado can be exemplified by the *strict sense* type (a species-rich dense biome of shrubs and trees, 8-10 m high, with a dense understory) (Durigan et al., 2002; Gottsberger and Silberbauer-Gottsberger, 2006). The Cerrado area studied by us has an average of 44.9% of the soil covered by grass, 5.8% by shrubs, 23.5% by small trees, and 8.8% by large trees, and has an average density of 17 *C. brasiliense* trees per ha. The pasture area has 84.2% of the soil covered by the African grass *Brachiaria decumbens* (Stapf), 0.2% by shrubs, 4.8% by small trees, 2.8% by large trees, and has an average of 42.3 *C. brasiliense* trees per ha. The urban area (university *campus*) has 100% of the soil covered by *Paspalum notatum* Flüggé grass and has an average of 100 *C. brasiliense* trees per ha (Leite et al., 2006). Therefore, the most plant species rich habitat is that of the native Cerrado vegetation, followed by the pasture and urban habitat, respectively (Leite et al., 2006).

2.2. Study host plants and galling species

Adult (reproductive phase) *C. brasiliense* trees in the Cerrado area were 4.1 ± 0.2 m tall (average ± SE) and had a crown width of 2.9 ± 0.1 m. In the pasture area, these trees were 5.2 ± 0.2 m tall and with a crown width of 4.0 ± 0.1 m, while in the urban environment, trees were 3.8 ± 0.2 m tall with a crown width of 1.7 ± 0.1 m, see (Leite et al., 2006).

The studied hymenopteran galls on *C. brasiliense* leaves are: i) *Eurytoma* sp. glodoid galls (Eurytomidae); ii) *Bruchophagus* sp. vein galls (Eurytomidae); iii) Eulophidae spherical galls; and iv) Hymenopteran discoid galls. For detailed information on the natural history of the galling insects and within tree distribution, the community of gall parasitoid, hyperparasitoid and predator insects can be found in Leite (2014).

2.3. Study design

The study design was completely randomized with 12 replicates (12 tree individuals) growing in three kinds of soils. At each site (sandy, average texture, and clayey soils), data were collected on *C. brasiliense* adult trees (producing fruits) at every 50 m along a 600 m transect. For the 12 repetitions, we collected data during three consecutive years to capture a greater number of insect species (e.g., rare species) in a given year or area. No fertilizers or pesticides were used in these areas.

The distribution of galling insects and their galls, predators, parasitoids, and percentage of leaves infested with galls (three leaflets/leaf) was recorded by examining 12 fully expanded leaves of the 36 *C. brasiliense* trees (one leaf in each vertical and horizontal stratifications of canopy) (Demolin-Leite et al., 2020). Sampling was performed in the morning (7:00-11:00 AM) by direct visual observation every month (Horowitz, 1993). Insects were collected with tweezers, brushes, or aspirators and preserved in vials with 70% alcohol for identification by taxonomists. The leaves were collected and transported to the laboratory. Gall size was measured by using a digital caliper (accurate to nearest 0.1mm). Leaves were scanned and the leaf area was calculated using Sigma Scan Pro software, and then we calculated the area of each leaf that was occupied by each galling species as a rough indication of herbivory (Demolin-Leite et al., 2020). Galling insects cause a large impact on the host plant because nutrients are moved from distant structures to the gall tissue (Fernandes, 1987), and hence this represents solely the local area impacted. Subsequently, leaves were placed inside a white plastic pot (temperature 25ºC), and for each collected sample, we evaluated the emergence of galling insects, parasitoids, and hyperparasitoids at every alternate day during the 30-day period. The emerged insects were collected and preserved as described above for identification by taxonomists. The voucher number for spiders is IBSP 36921-36924 (Instituto Butantan, São Paulo state, Brazil) and for insects, the voucher numbers are 1595/02 and 1597/02 (CDZOO, Universidade Federal do Paraná, Paraná state, Brazil).

The ecological indexes (abundance, species richness and diversity) were calculated for the arthropods identified. These indexes were calculated with the taxa dataset analyzed in the BioDiversity Pro software (McAleece et al., 1997). The abundance was obtained with the average of each species/tree, the diversity using the Hill formula and the species richness using the Simpson index (Hill, 1973; Jost, 2006; Begon et al., 2007; Lazo et al., 2007). *Caryocar brasiliense* leaves in Cerrado, pasture, and urban areas differed in many galling insect and parasitoid community attributes (Demolin-Leite et al., 2020).

2.4. Statistical analyses

Abundance averages were realized by reducing the data per leaflet/tree in each area. Correlations of the abundance, species richness and diversities of galling insect, parasitoids, and predators, number of galling insects and their galls, predators and parasitoids with physical and chemical characteristics of the soils (Leite et al., 2006; Demolin-Leite et al., 2020) were subjected to principal component regressions (PCR) ($P < 0.05$). The regression model known as PCR, or regression on principal components, uses principal component analysis, based on the covariance matrix, to perform regression (Bair et al., 2006). Thus, it can reduce the regression dimension by excluding the dimensions that contribute to causing multicollinearity problem, that is, linear relationships between the independent variables.

The parameters used in these regressions were those significant (P < 0.05) for the selection of the variables for the method “Stepwise”. The data presented are statistically significant (P <0.05).

3. Results

Caryocar brasiliense trees in soils with the lowest capacity of cationic exchange (C.C.E.) and the highest percentage of sand showed the highest species richness and diversity of galling insects, while soils with the greatest phosphorus content and the smallest percentage of sand (more available water) had the highest abundance of galling insects (Figure 1A-1C). Plants of *C. brasiliense* in soil with a more clayey texture and higher pH showed a higher number of leaflets attacked by gall-forming species (*Eurytoma* sp. galls = 85.87 ± 3.42% of all galls) (Figure 1D). The area occupied by gall structure in each leaflet was higher in plants localized in soils with higher C.C.E. and aluminum content (Figure 1E). The highest adult emergence of gall-forming *Eurytoma*

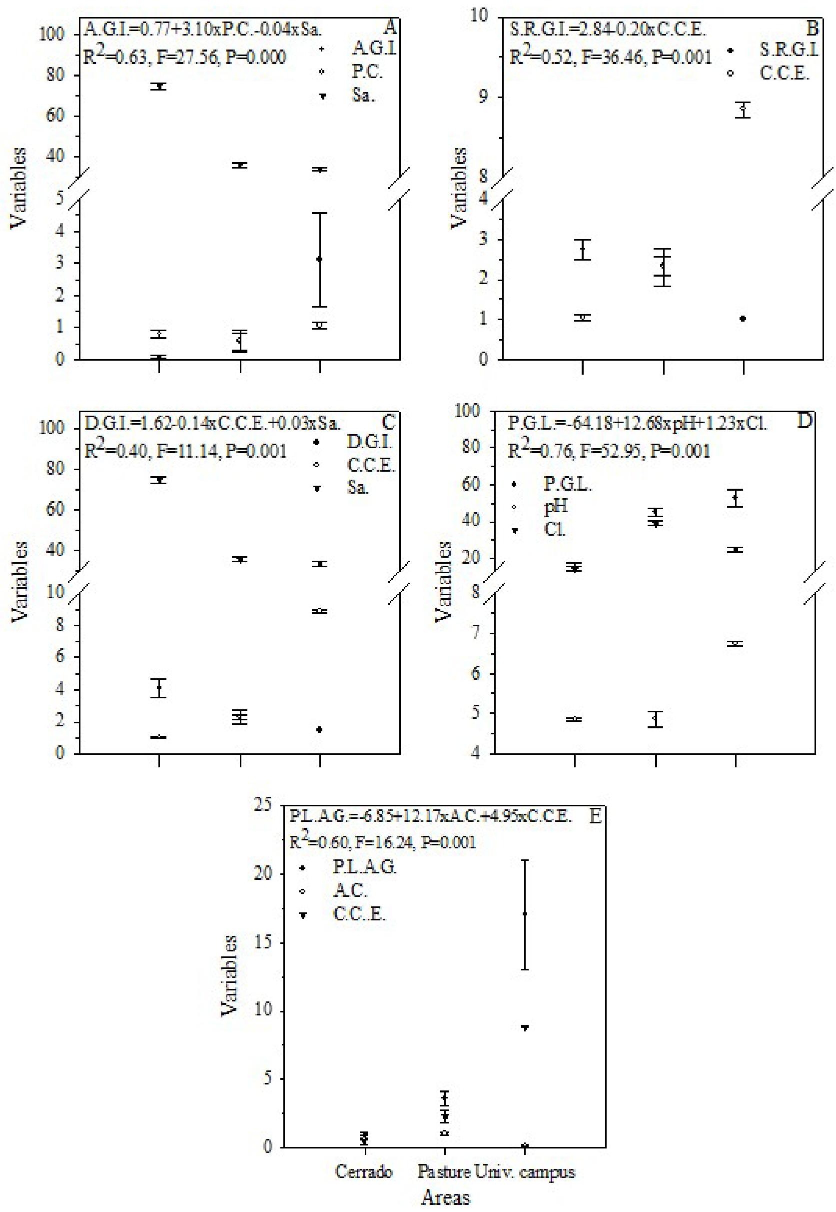

Figure 1. Principal components regressions among: (A) abundance of galling insects (A.G.I.) with phosphorus-Mehlich 1 (mg dm^{-3}) contents (P.C.) and sand (dag kg^{-1}) (Sa.); (B) species richness of galling insects (S.R.G.I.) with capacity of cationic exchange ($cmol_c$ dm^{-3}) (C.C.E.); (C) diversity of galling insects (D.G.I.) with C.C.E. and Sa.; (D) percentage of galled leaflet by all galls (P.G.L.) with pH in water and clay (dag kg^{-1}) (Cl.); and (E) percentage of leaflet area taken by all galls (P.L.A.G.) with aluminum ($cmol_c$ dm^{-3}) contents (A.C.) and C.C.E. on *Caryocar brasiliense* trees in three years. The symbols represent the averages and the bars the standard errors. n = 111.

sp. (91.98 ± 4.52% of galling insects that emerged in the laboratory) was observed in leaflets of *C. brasiliense* from the soils with the highest values of phosphorus content and percentage of silt. The number of globoid galls induced by *Eurytoma* sp. was higher in soils with higher pH, C.C.E., and phosphorus content. The length and width of gall conglomerates (morphological structure characterized by the agglomeration of individual galls close together) and the size of globoid galls (mm^2) was higher in soils with the most elevated pH and percentage of clay (Figure 2A-2E). The number of Hymenopteran discoid galls (H.D.G.) showed a negative correlation with the capacity of cationic exchange. On the other hand, H.D.G. was positively related to higher aluminum content and soil base saturation (S.B.B.), a soil property representing the percentage of C.C.E. occupied by base cations at pH 7.0 (Figure 2F).

The abundance of galling insect parasitoids was positively affected by their galling insect hosts abundance.

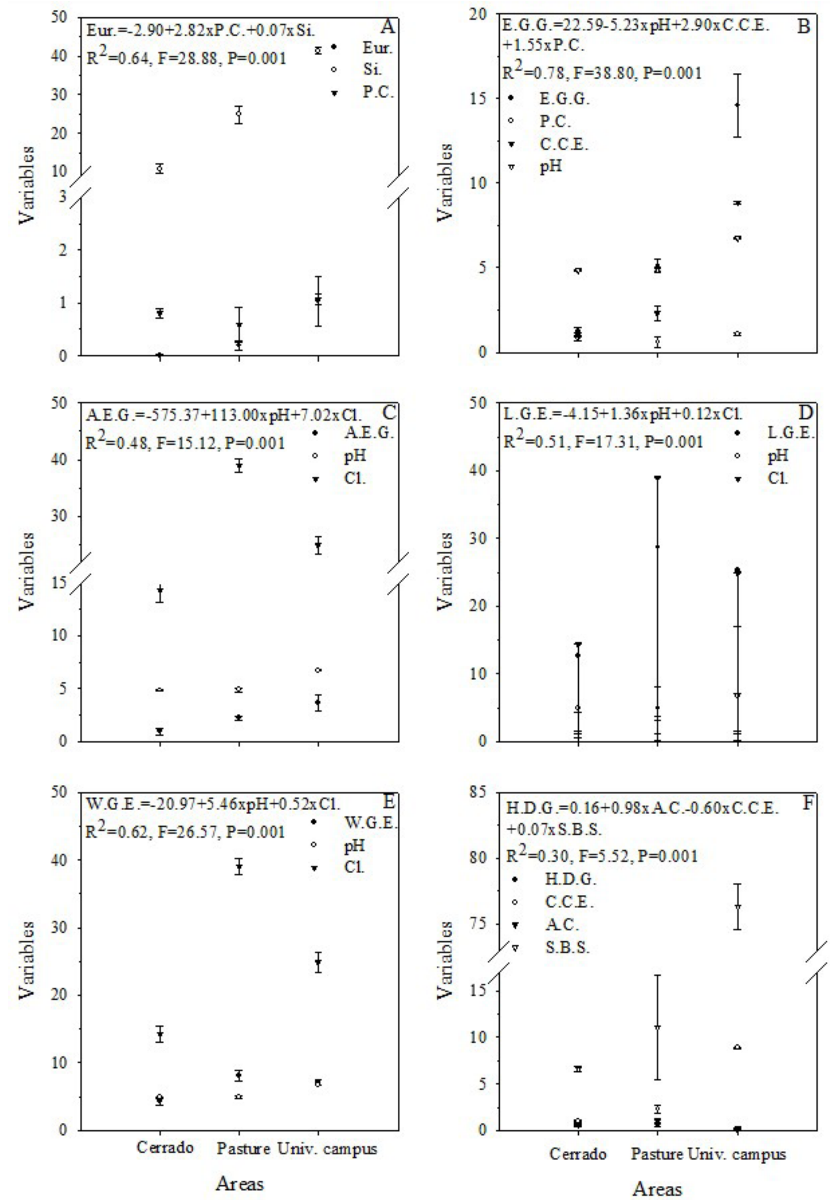

Figure 2. Principal components regressions among: (A) *Eurytoma* sp. galling insect adults (Eur.) with phosphorus-Mehlich 1 (mg dm^{-3}) contents (P.C.) and silt (dag kg^{-1}) (Si.); (B) numbers of *Eurytoma* sp. glodoid galls (E.G.G.) with pH in water, capacity of cationic exchange ($cmol_c$ dm^{-3}) (C.C.E.), and P.C.; (C) area (mm^2) of *Eurytoma* sp. glodoid galls (A.E.G.) with pH and clay (dag kg^{-1}) (Cl.); (D) length of conglomerate of *Eurytoma* sp. globoid galls (L.G.E.) with pH and Cl.; (E) width of conglomerate of *Eurytoma* sp. globoid galls (W.G.E.) with pH and Cl.; and (F) number of Hymenopteran discoid galls (H.D.G.) with aluminum ($cmol_c$ dm^{-3}) contents (A.C.), C.C.E., and percentage of soil base saturation of the capacity of cationic exchange to pH 7.0 (S.B.S.) on *Caryocar brasiliense* trees in three years. The symbols represent the averages and the bars the standard errors. n = 111.

Soil pH and galling insect richness positively impacted parasitoid species richness. On the other hand, parasitoid richness was negatively affected by the percentage of sand. The diversity of parasitoids on *C. brasiliense* trees was positively affected by the diversity of galling insect and percentages of silt and clay (Figure 3A-3C). The abundance of *Sycophila* sp. (Hymenoptera: Eurytomidae) (91.36 ± 3.99% of *Eurytoma* sp. parasitoids emerged in the laboratory) was positively influenced by *Eurytoma* sp. adults. But its abundance was negatively affected by *Ablerus magistretti* Blanchard (Hymenoptera: Aphelinidae) (*Eurytoma* sp. parasitoids). The parasitoid *A. magistretti* was positively affected by the galling *Eurytoma* sp. adults, phosphorus content and percentage of silt. However, its abundance was negatively affected by the number of *Sycophila* sp. adults, aluminum content and pH (Figure 3D-3E).

The abundance of predators was positively affected by the phosphorus content and percentage of clay in the soil. The species richness of predators was positively affected by the number of H.D.G., the species richness

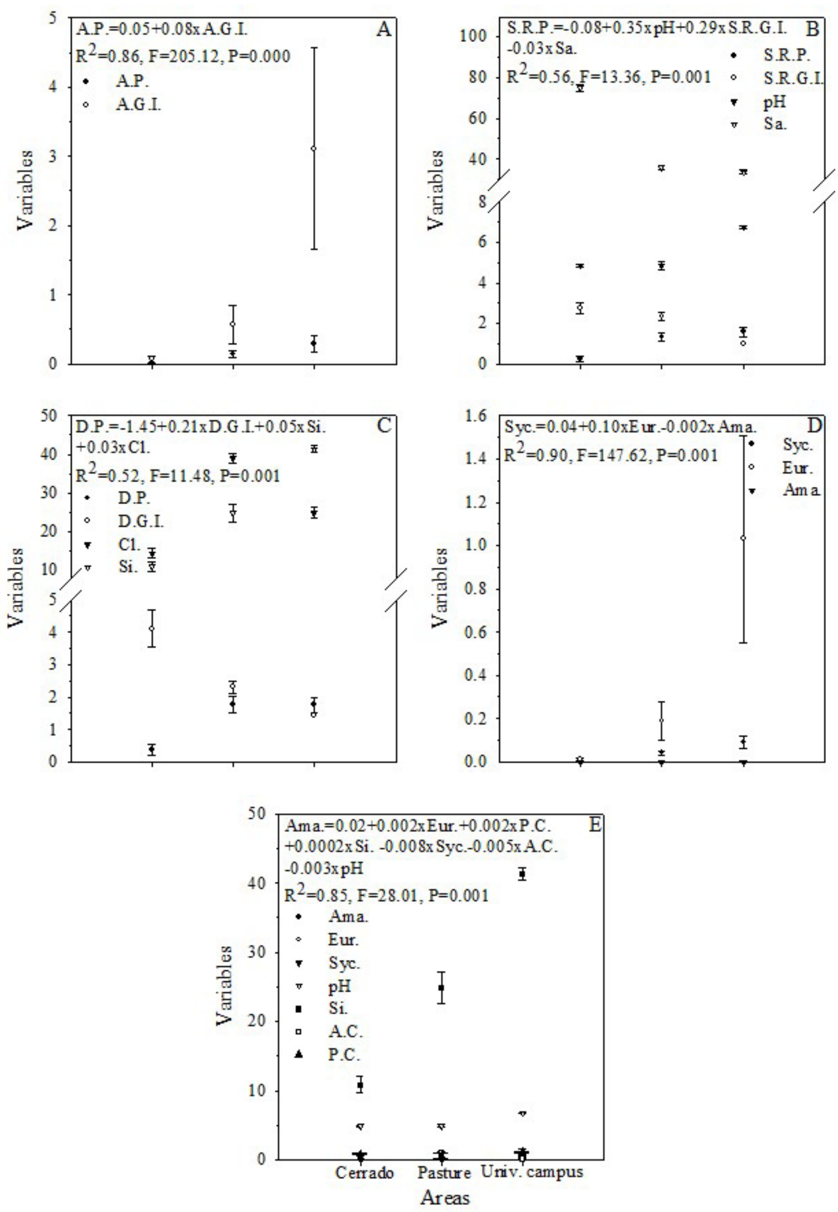

Figure 3. Principal components regressions among: (A) abundance of parasitoids (A.P.) with abundance of galling insects (A.G.I.); (B) species richness of parasitoids (S.R.P.) with pH in water, species richness of galling insects (S.R.G.I.), and sand (dag kg^{-1}) (Sa.); (C) diversity of parasitoids (D.P.) with diversity of galling insects (D.G.I.), silt (dag kg^{-1}) (Si.), and clay (dag kg^{-1}) (Cl.); (D) *Sycophila* sp. adults (Syc.) with *Eurytoma* sp. galling insect adults (Eur.) and *Ablerus magistretti* adults (Ama.); and (E) Ama. with Eur., phosphorus-Mehlich 1 (mg dm^{-3}) contents (P.C.), Si., Syc., aluminum ($cmol_c$ dm^{-3}) contents (A.C.), and pH on *Caryocar brasiliense* trees in three years. The symbols represent the averages and the bars the standard errors. n = 111.

of galling insect parasitoids, and the percentage of clay. The diversity of predators was positively affected by the diversity of galling insect parasitoids and the percentage of clay in the soil (Figure 4A-4C). The predator *Zelus armillatus* (Lep. & Servi) (Hemiptera: Reduviidae) (15.83 ± 4.33% of all predators) was positively affected by phosphorus content, S.B.B., silt, and the number of *Eurytoma* sp. galls. On the other hand, this predator was negatively affected by the C.C.E. of the soil. Abundances of *Epipolops* sp. (Hemiptera: Geocoridae) and spiders were positively affected by protocooper ants (Hymenoptera: Formicidae). The percentage of silt in the soil showed a positive correlation with spiders. On the other hand, *Epipolopus* sp. and predators bugs were positively affected by clay percentage in soil. Soils with more phosphorus content contributed positively to spiders and predators bugs population, while *Epipolops* sp. was negatively correlated with pH (Figure 4D-4F).

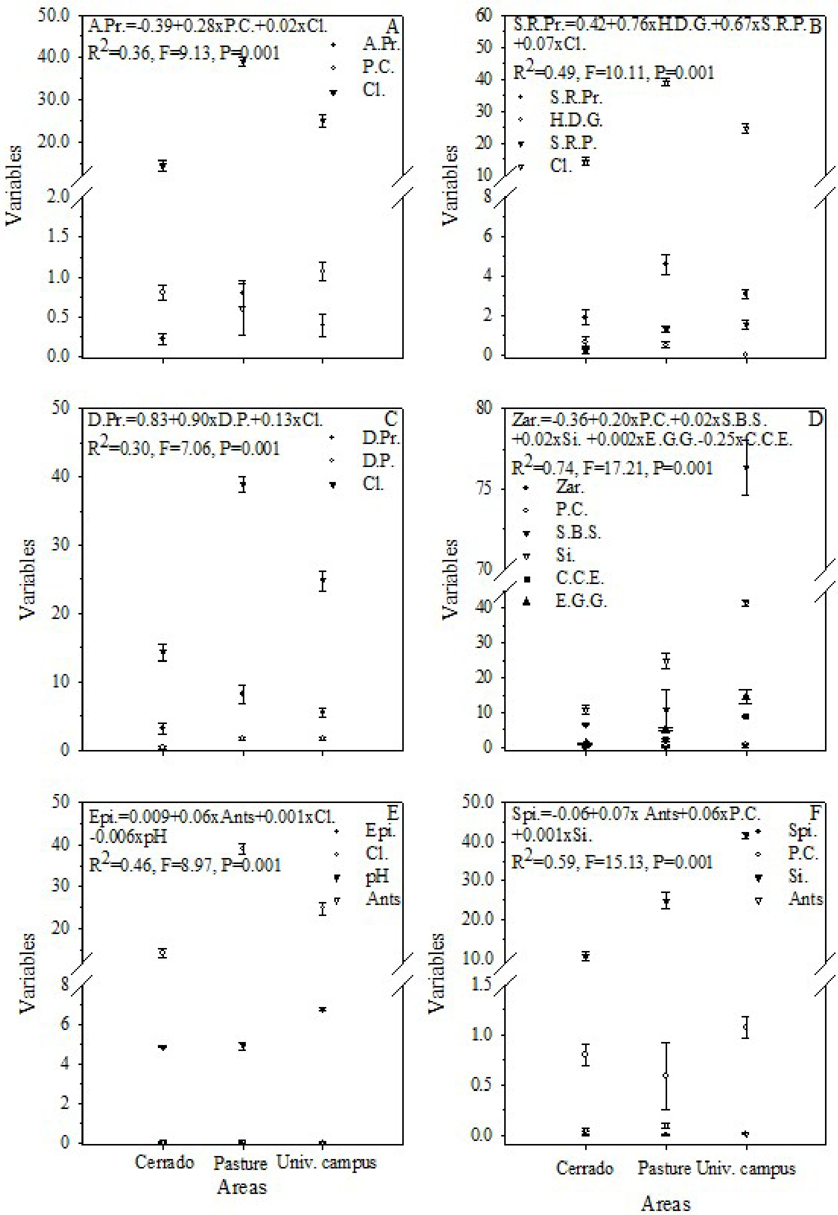

Figure 4. Principal components regressions among: (A) abundance of predators (A.Pr.) with phosphorus-Mehlich 1 (mg dm^{-3}) contents (P.C.) and clay (dag kg^{-1}) (Cl.); (B) species richness of predators (S.R.Pr.) with number of Hymenoptera discoid galls (H.D.G.), species richness of parasitoids (S.R.P.), and Cl.; (C) diversity of predators (D.Pr.) with diversity of parasitoids (D.P.) and Cl.; (D) number of *Zelus armillatus* (Zar.) with P.C., percentage of soil base saturation of the capacity of cationic exchange to pH 7.0 (S.B.S.), silt (dag kg^{-1}) (Si.), numbers of *Eurytoma* sp. glodoid galls (E.G.G.), and capacity of cationic exchange ($cmol_c$ dm^{-3}) (C.C.E.); (E) number of *Epipolops* sp. (Epi.) with protocooperanting ants (Ants), Cl., and pH in water; and (F) number of spiders (Spi.) with Ants, P.C., and Si. on *Caryocar brasiliense* trees in three years. The symbols represent the averages and the bars the standard errors. n = 111.

4. Discussion

In this study, we evaluated the relationship between physical and chemical soil properties and the ecological indices of galling insects and their natural enemies in *Caryocar brasiliense* trees. To test the hypothesis proposed in this work, we classified the qualitative aspects of soils (better or worse nutritional quality for plants) through their physical and chemical properties. Thus, it was possible to observe the impact of these characteristics on the population dynamics of galling insects and their natural enemies. For example, the highest species richness and diversity of galling species and their predators were observed on *Caryocar brasiliense* trees present in soils with the lowest capacity of cationic exchange and the highest percentage of sand, corroborating with the habitat stress hypothesis at the plant level (Fernandes and Price, 1988).

Caryocar brasiliense trees in soils with unsuitable chemical properties (e.g., lower capacity of cationic exchange) and worse textures (e.g., sandy) showed higher species richness and diversity of galling species. We considered soils with the worst texture according to the potential risk to cause water stress on plants (Fernandez-Illescas et al., 2001; Bruand et al., 2005). These soils were classified from highest to lowest potential as sandy textured soils (Cerrado area), medium textured soils (silt - urban area) and clayey soils (pasture). Clayey and sandy soils were more acidic, while clayey soils were richer in aluminum and sum of bases. On the other hand, the medium-textured soil contained higher silt and a more compacted texture compared to other soils (sandy and clayey) (Leite et al., 2006).

The availability of water and nutrients are abiotic factors that affect stress levels in plants. According to the plant stress hypothesis, more stressed plants have a lower capacity to synthesize defensive chemicals and, consequently, increase their susceptibility to insect attack (Bruyn, 1995; Fernandes et al., 1994). Therefore, this impairment in plant defense mechanisms potentially results in greater abundance, survival, and richness of galling insect species (Gonçalves-Alvim and Fernandes, 2001; Fernandes et al., 1994; Orians and Fritz, 1996). Regarding species richness and diversity of galling insects, our results agreed with several studies that reported a higher diversity and species richness of galling insects in soils with lower fertility (determined by chemical characteristics) (Gonçalves-Alvim and Fernandes, 2001; Cuevas-Reyes et al., 2003; Cuevas-Reyes et al., 2014). When areas with different vegetation, soil, and topography but similar rainfall were compared, Cuevas-Reyes et al. (2003) found the lowest number of plants with galls in soils richest in phosphorus contents (more fertile). Additionally, Cuevas-Reyes et al. (2014) observed the highest number of plants with galls and the highest number of galls per plant in sites with low phosphorus levels (lower fertile), similar to the Cerrado area, where the poorest soil was recorded.

We found a negative correlation between the species richness of gall-inducing insects and the availability of phosphorous and nitrogen. Cuevas-Reyes et al. (2003) found similar results in more fertile soils that affected the spatial distribution of galling insects and contributed negatively to the abundance at the community level. Our results showed that the species richness of galling insects was negatively correlated with soil levels of magnesium, potassium, and zinc, corroborating the soil fertility hypothesis (Gonçalves-Alvim and Fernandes, 2001). The levels of magnesium, potassium, iron contents, and cation exchange capacity explained 72% of the variation in the species richness of galling insects (Gonçalves-Alvim and Fernandes, 2001). Overall, the results corroborate the hypothesis that habitat stress is an important factor that generates the patterns of galling insect species richness in the Brazilian Cerrado (Gonçalves-Alvim and Fernandes, 2001).

In contrast to species richness and diversity indices, the abundance of *Eurytoma* sp. (most abundant galling insect, ≈92%) – adults and/or its galls (≈86% of all galls) was correlated with a higher concentration of phosphorus, pH, and silt (e.g., urban area) or clay of the soils (e.g., pasture area). Additionally, *C. brasiliense* trees were more leaflets galled and had the largest leaf surface occupied by galls, indicating higher gall density in these soils.

Our results showed that soils with better chemical characteristics (e.g., higher pH and phosphorus content) and physical conditions (lower sand content) contributed to higher species richness and diversity of parasitoids. These soil properties also showed a positive relationship with the abundance of *Sycophila* sp. and *A. magistretti* (both parasitoids of *Eurytoma* sp.). Therefore, the abundance of galling insect parasitoids was directly correlated with *Eurytoma* sp. This correlation provides support for the hypothesis that higher mortality caused by natural enemies occurs in mesic habitats (Fernandes and Price, 1992). Furthermore, the distribution patterns suggest that the *Sycophila* sp. and *A. magistretti* have high dispersal ability and can efficiently follow their hosts to where these are most numerous. Interestingly, *C. brasiliense* trees localized in soils with better chemical and physical conditions were more affected by abundance of *Eurytoma* sp. galls despite the greater abundance of parasitoids. It was expected that the greater abundance of parasitoids would result in less gall infestation (Morris et al., 2005; Samková et al., 2019; Venturino et al., 2008). However, our findings suggest that *Eurytoma* sp. has an efficient anti-predator defense to prevent population decline, possibly reducing the per capita risk of parasitism (Low, 2008).

The predator/prey interaction exhibited a distribution pattern similar to parasitoids on *C. brasiliense*. All predators' abundance, richness, and species diversity followed the trend of populational distribution of their prey, showing a greater level of these ecological indices in soils with higher phosphorus contents (urban area) and percentage of clayey or silt soils (pasture and urban areas). This distribution pattern also included *Z. armillatus* (≈16% of all predators), the main predator of *Eurytoma* sp.. Again, these data provide support for the enemy hypothesis on the distribution of galling insects (Fernandes and Price, 1992). The highest numbers of the predator *Z. armillatus* on *C. brasiliense* trees in the University *Campus* might be due to these trees having more galled leaves by *Eurytoma* sp. than in the pastureland and Cerrado habitats (Leite, 2014). *Zelus armillatus* was observed preying upon *Eurytoma* galls, which can colonize up to 70% of the leaf area with galls

(Leite, 2014). The greater species richness and diversity of predators and the abundance of *Epipolops* sp. and spiders were observed in more clayey soils (pasture area), and the opposite was observed in soils with higher sand content (Cerrado area).

On the contrary to the habitat stress hypothesis, low soil fertility negatively affected predators' species richness and diversity. Following an opposite pattern to diversity and species richness, the abundance indices of the gall-forming *Eurytoma* sp., and their main parasitoids (e.g., *Sycophila* sp.) and the predator (e.g., *Z. armillatus*) were recorded in better soil habitats. Our data indicate the importance of habitat quality in galling insect community composition and the impact of the soil properties in mediating these insects' distribution on *C. brasiliense*.

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