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Distribution of insect galls in xeric and mesic habitats of Floresta Nacional de Silvânia, Brazil

Bárbara Araújo Ribeiro Bergamini¹, Leonardo Lima Bergamini¹, Benedito Baptista dos Santos¹ & Walter Santos de Araújo²

- 1. Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Goiânia, GO, Brazil.
- 2. Departamento de Biologia Geral, Centro de Ciências Biológicas e da Saúde, Universidade Estadual de Montes Claros, Montes Claros, MG, Brazil. (walterbioaraujo@yahoo.com.br)

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ABSTRACT. We investigated the insect gall distribution along savanna (xeric) and forest (mesic) vegetation in the Floresta Nacional de Silvânia, Goiás, Brazil. We tested if the insect gall diversity is higher in the xeric vegetation than in the mesic vegetation, as predicted by the hygrothermal stress hypothesis. The insect gall fauna was surveyed between December 2009 and June 2010 in two transects established each vegetation type. In total we found 186 insect gall morphotypes, distributed on 35 botanical families and 61 plant species. Cecidomyiidae (Diptera) induced the most insect galls (34.1%), and the plant family Fabaceae had the greatest richness of insect gall morphotypes (18). We recorded 99 insect gall morphotypes in the forest and 87 morphotypes in the savanna vegetation, being that none insect gall morphotype occurred in both habitats. We found that the insect gall richness and abundance did not differ between forest and savanna transects. On the other hand, the estimated insect gall richness was higher in the forest than in the savanna. Our findings contrary the hygrothermal stress hypothesis possibly because forest habitats have higher plant architecture complexity and occurrence of super-host taxa than the savanna habitats.

KEYWORDS. Cecidomyiidae, Cerrado, Fabaceae, plant-insect interaction.

RESUMO. Distribuição de galhas de insetos em habitats xéricos e mésicos da Floresta Nacional de Silvânia, Brasil. Foi inventariada a distribuição de galhas de insetos ao longo de vegetações savânicas (xéricas) e florestais (mésicas) na Floresta Nacional de Silvânia, Goiás, Brasil. O estudo testou se a diversidade de insetos galhadores é maior na vegetação xérica do que na vegetação mésica, como predito pela hipótese do estresse higrotermal. A fauna de galhadores foi amostrada entre dezembro de 2009 e junho de 2010 em dois transectos estabelecidos em cada tipo de vegetação. No total foram encontrados 186 morfotipos de galhas de insetos, distribuídos em 35 famílias e 61 espécies de plantas. Cecidomyiidae (Diptera) induziu a maioria das galhas de insetos (34,1%) e a família Fabaceae teve a maior riqueza de morfotipos de galhas (18). Foram registrados 99 morfotipos de galhas de insetos na floresta e 87 morfotipos no cerrado, sendo que nenhum morfotipo de galha ocorreu em ambos os habitats. A riqueza e a abundância de galhas de insetos não diferiram entre os transectos de floresta e cerrado. Por outro lado, a riqueza estimada de galhas de insetos foi maior na floresta do que no cerrado. Esses resultados contrariam a hipótese do estresse higrotermal possivelmente devido aos habitats florestais apresentarem maior complexidade arquitetônica das plantas e ocorrência de táxons super-hospedeiros do que os hábitats savânicos.

PALAVRAS-CHAVE. Cecidomyiidae, Cerrado, Fabaceae, interação inseto-planta.

The Brazilian Cerrado contains a wide variety of vegetation types, ranging from forests to typical grassland formations (RIBEIRO & WALTER, 2008). This great vegetation heterogeneity in the Cerrado is caused by several factors, mainly variations in fire, climate, water availability and soil fertility (OLIVEIRA-FILHO & RATTER, 2002). In this context, the Cerrado constitutes a mosaic of phytophysiognomies, with many mesic (i.e., non-sclerophyllic and rich in water and nutrients) and xeric (i.e., sclerophyllic and poor in water and nutrients) vegetation types. These environmental differences between xeric and mesic habitats can directly affect the distribution of insect herbivores (Neves *et al.*, 2010; Leal *et al.*, 2015), such as the highly specialized gall-inducing insects (Araújo *et al.*, 2014).

Comparisons between mesic and xeric vegetation in the Cerrado have pointed to a higher galling insect

richness in the latter type (review in Araújo et al., 2014), as proposed by the hygrothermal stress hypothesis (Fernandes & Price, 1988). Plants under environmental stress condition of xeric habitats tend to accumulate higher concentrations of secondary metabolites (Araújo et al., 2014). Because galling insects can sequester the plant secondary metabolites during gall formation as a protection mechanism against natural enemies (Cuevas-Reyes et al., 2004, 2011; Gonçalves-Alvim & Fernandes, 2001), evidences pointed that this high defense investment of xeric habitat plants favors insect gall occurrence (Fernandes & Price, 1988; Gonçalves-Alvim et al., 2001; Lara et al., 2002).

Contrary to the predictions of the hygrothermal stress hypothesis, some studies have not found the pattern

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of the greatest richness of insect galls in xeric habitats when compared with mesic habitats of Cerrado (e.g., Araújo & Santos, 2008; Mendonça, 2011). These studies attribute their results to tendency in mesic vegetation to have greater structural complexity, including higher canopy strata, which can increment the insect gall diversity (Fleck & Fonseca, 2007). Besides that, the occurrence of host plants that exhibit a high intrinsic diversity of galling insects in the mesic vegetation (i.e., super-host taxa) (Araújo et al., 2014), can make these habitats more rich in insect galls than xeric habitats.

In the present study we performed an inventory of gall-inducing insects and their host plants in two contrasting vegetation types of Cerrado, savanna (xeric) and forest (mesic), located in the Floresta Nacional de Silvânia (Flona-Silvânia), Brazil. Thus, we tested if the richness and abundance of the insect galls is higher in the xeric vegetation than in the mesic vegetation, as predicted by the hygrothermal stress hypothesis.

MATERIAL AND METHODS

Study area. The Flona-Silvânia is located in the city of Silvânia, state of Goiás, Midwest Brazil (Fig. 1). The climate of the region is classified as Aw of Köppen (ALVARES et al., 2013), being humid tropical with well-defined dry (April to September) and rainy (October to March) seasons. The area of the park is of 466.55 ha being mostly composed by a flat tableland at 900 m asl (Francener et al., 2012). The Flona-Silvânia exhibits almost all types of Cerrado vegetation, but mainly typical savanna and forest (gallery forest and semidecidual forest), which occupy 70% of the park area (Araújo et al., 2012) (Fig. 2). The study was concentrated in two areas of the Flona-Silvânia, being one with xeric habitat (16°38'11.79"S and 48°39'50.82"W) and other with mesic habitat (16°37'52.90"S and 48°39'52.38"W). The xeric habitat (Fig. 3) is a typical savanna vegetation characterized by spaced trees and a matrix of shrubs and grasses, while the mesic habitat (Fig. 4) is a gallery forest, located on the banks of a stream and dominated by trees and high and closed canopy (Araújo et al., 2012). These two vegetation types differ in the structure and in the floristic composition (RIBEIRO & WALTER, 2008).

Insect gall sampling. We performed four bi-monthly samplings between December 2009 and June 2010 in the two vegetation types. The insect gall sampling was done through active searches, with duration of 01h30min, along four fixed transects, being two in each vegetation type (ARAÚJO et al., 2011). In each transect, we sampled every plant that hosted insect galls, including trees, shrubs and herbs. All insect galls encountered were recorded, photographed, collected and placed individually in labeled plastic bags for transportation to the laboratory. Plant fragments of each host plant were collected, part of the material being sent for botanical identification, the remainder being used for obtains the immature and adult insects, in the laboratory.

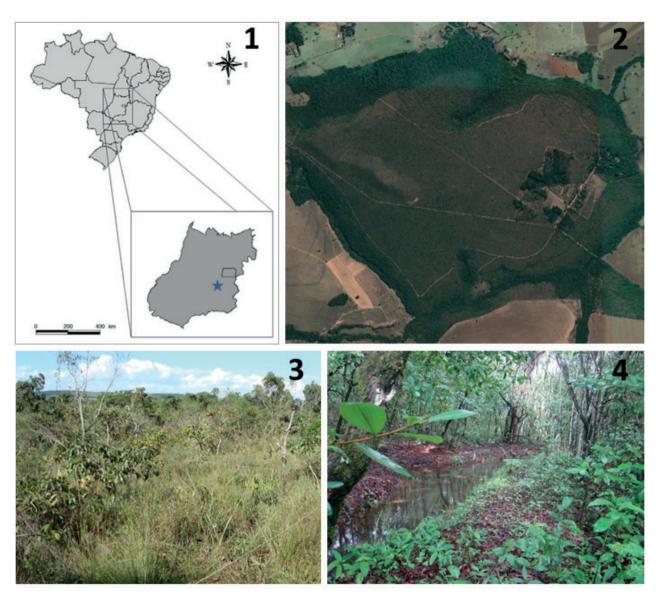
Insect galls were classified into morphotypes using the host plant species and external morphology (organ of occurrence, form, colour, pubescence and size) (ARAÚJO et al., 2011). Gall morphotypes were used as a surrogate for species of gall-inducing insects because there is a consensus in the literature about host-specificity and morphological-fidelity of insect galls (reviewed in Carneiro et al., 2009). All gall morphotypes were deposited in the insect gall collection of the Laboratório de Entomologia at Universidade Federal de Goiás. Sampling resulted in three descriptive variables for insect gall diversity: insect gall richness, number of galled plants and number of insect gall morphotypes per plant species. We used the variable number of galled plants as an indirect measure of insect gall abundance (Dalbem & Mendonça, 2006).

Data analyses. For statistical analyses we used insect gall data recorded in the four sampling transects along four sampling campaigns. A sample-based species accumulation curve (collector curve) was built using the observed galling species richness and the galling species richness estimated from 1st order Jackknife estimator. This curve was used to access to which extent sampling sufficiency was achieved. Insect gall richness, abundance and number of gall morphotypes per host plants were compared between savanna and forest habitats using *t*-tests. Additionally, we also compared the number of sampled host plants and the estimated galling species richness between savanna and forest transects. Assumptions of normality and homoscedasticity were previously tested for all analyses.

RESULTS

We found a total of 186 insect gall morphotypes from five insect orders, and 61 species of host plants from 35 plant families in the Flona-Silvânia (Tab. I). Gall-inducing insects belonged to Coleoptera, Diptera, Hemiptera, Lepidoptera and Thysanoptera, with Cecidomyiidae (Diptera) being the most common insect taxon having induced 34.1% of the gall morphotypes. The plant families that showed the greatest richness of insect galls were Fabaceae, with 18 morphotypes, Asteraceae with 17 and Sapindaceae with 16 morphotypes (Tab. I). The plant species *Protium heptaphyllum* (Aubl.) Marchand (Burseraceae), Siparuna guianensis Aubl. (Siparunaceae) and Serjania sp. (Sapindaceae) were the most diverse host species with 14, 12 and 12 insect gall morphotypes, respectively. Most of the insect galls occurred on leaf lamina (68.2%), and were ellipsoids (38.7%), greens (38.7%) and glabrous (37.6%).

Ninety-nine gall morphotypes (52.2%) were collected in the forest and 87 (46.8%) in the savanna, being that none insect gall morphotype occurred in both habitats (Tab. II; Fig. 5). The host families with higher diversity of insect galls were Asteraceae (17), Fabaceae (11) and Malpighiaceae (8) in the savanna and Burseraceae (14), Siparunaceae (11) and Sapindaceae (10) in the forest (Tab. I). The insect gall sampling was relatively good in view of the large diversity



Figs 1-4. Location and characterization of the study area: 1, location of the Flona-Silvânia (marked by the star) in the city of Silvânia, State of Goiás, Midwest of Brazil; 2, map of the Flona-Silvânia showing the areas of savanna (clear areas) and forest (dark areas); 3, characterization of the xeric habitat composed by typical savanna vegetation; 4, characterization of the mesic habitat composed by gallery forest vegetation.

of galling insects and host plants studied (Fig. 6), although savanna being better sampled than the forest area. The average number of gall morphotypes per plant species was 2.41 (\pm 3.39 SD) for savanna and 3.41 (\pm 1.81 SD) for forest, but this values did not differ statistically (t = 1.51; p = 0.13). The number of sampled host plants also did not differ between forest and savanna habitats (t = -1.83; p = 0.08).

We did not find differences between forest and savanna transects concerning insect gall richness (t = -1.74; p = 0.10) and abundance (t = -0.53; p = 0.34). Insect gall richness by transect in the savanna was on average 20.23 (\pm 5.84 SD) morphotypes, and in the forest 24.25 (\pm 2.76 SD) gall morphotypes. The average abundance of insect galls by transect in the savanna was of 37.8 (\pm 8.38 SD) and in the forest was of 40.5 (\pm 5.75 SD). On the other hand, the estimated insect gall richness was higher in the forest than

in the savanna (Fig. 7). The estimated number of insect gall species was of 195.6 (\pm 6.47 SD) for forest and 130.5 (\pm 7.93 SD) for savanna.

DISCUSSION

Previous studies have indicated higher insect gall richness in the xeric habitats than mesic habitats of the Brazilian Cerrado (Gonçalves-Alvim & Fernandes, 2001; Lara et al., 2002; Araújo et al., 2011), as predicted by the hygrothermal stress hypothesis (Fernandes & Price, 1988). According to this hypothesis, in xeric environments the plants are more nutritive for galling insects and the attack frequency of natural enemies (e.g., parasitoids) is lower when compared to mesic habitats (Fernandes & Price, 1988; Araújo et al., 2014). Contrary to expectations, we

Tab. I. Number of insect gall morphotypes and host plant species in the different host plant families recorded forest (mesic) and savanna (xeric) vegetation in the Flona-Silvânia, Goiás, Brazil.

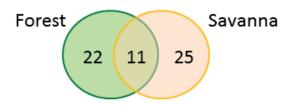
Host plant family	Insect gall richness			Plant species richness		
	Forest vegetation	Savanna vegetation	Total	Forest vegetation	Savanna vegetation	Total
Acanthaceae	4	0	4	1	0	1
Anacardiaceae	1	2	3	1	1	2
Annonaceae	2	0	2	1	0	1
Apocynaceae	0	3	3	0	2	2
Asteraceae	0	17	17	0	4	4
Bignoniaceae	3	1	4	1	1	2
Burseraceae	14	0	14	1	0	1
Celastraceae	10	0	10	1	0	1
Chrysobalanaceae	1	0	1	1	0	1
Clusiaceae	0	2	2	0	1	1
Connaraceae	0	2	2	0	1	1
Dilleniaceae	4	3	7	2	1	3
Ebenaceae	0	1	1	0	1	1
Erythroxylaceae	1	4	5	1	2	3
Euphorbiaceae	0	1	1	0	1	1
Fabaceae	7	11	18	3	3	6
Flacourtiaceae	0	1	1	0	1	1
Lamiaceae	0	2	2	0	2	2
Lauraceae	3	0	3	2	0	2
Loganiaceae	0	1	1	0	1	1
Lythraceae	0	1	1	0	1	1
Malpighiaceae	0	8	8	0	2	2
Malvaceae	3	0	3	1	0	1
Melastomataceae	1	0	1	1	0	1
Meliaceae	2	0	2	2	0	2
Monimiaceae	2	0	2	1	0	1
Myrtaceae	7	7	14	1	3	4
Ochnaceae	1	1	2	1	1	2
Piperaceae	1	0	1	1	0	1
Proteaceae	3	2	5	1	1	2
Rubiaceae	8	2	10	2	2	4
Salicaceae	0	2	2	0	1	1
Sapindaceae	10	6	16	2	1	3
Siparunaceae	11	1	12	1	1	2
Styracaceae	0	3	3	0	1	1
Vochysiaceae	0	3	3	0	1	1
Total	99	87	186	29	37	66

Tab. II. Distribution of insect gall richness, insect gall abundance and plant species richness between the sampling transects in mesic and xeric vegetation in the Flona-Silvânia, Goiás, Brazil.

Vegetation type	Transect	Insect gall richness	Insect gall abundance	Plant species richness
Mesic vegetation	Transect 1	60	110	25
	Transect 2	66	164	23
	Sub-total	99	274	29
Xeric vegetation	Transect 1	73	183	24
	Transect 2	53	114	28
	Sub-total	87	297	37
Total		186	571	61

found that the observed richness and abundance of insect galls did not differ between the two habitat types, but that the estimated richness of insect galls is greater for forest vegetation (mesic habitat). A possible explanation for the absence of differences in the insect gall observed diversity between xeric and mesic habitats is related to higher plant structural complexity in the forest environments. Gall-inducing insects usually have

Host plant families



Host plant species



Insect gall morphotypes



Fig. 5. Venn diagrams of the host plant families, host plant species and insect gall morphotypes occurring in the forest and savanna habitats of the Flona-Silvânia, Goiás, Brazil.

a preference for particular individuals (Lara et al., 2008), and parts of their host plant (Cuevas-Reyes et al., 2004; Santos et al., 2008), in order to optimize performance and offspring survival. There are evidences that structurally most complex host plants provide more resources for galling insects and have higher availability of oviposition sites for females (Gonçalves-Alvim & Fernandes, 2001; Lara et al., 2008; Araújo & Santos, 2009). Based on this perspective, plants with higher architecture should support a greater diversity of galling insects. Because forest habitats have a higher number of trees than savannas, these can increment significantly the insect gall richness in these environments (Araújo & Santos, 2008).

A consistent pattern observed in the Cerrado is that Fabaceae and Asteraceae are the most important host plant families of insect galls (Gonçalves-Alvim & Fernandes, 2001; Maia & Fernandes, 2004; Santos *et al.*, 2010; Araújo *et al.*, 2011; Malves & Frieiro-Costa, 2012). The main reason for the great gall richness hosted by these families is its high number of plant species (Mendonça *et al.*, 2008; Araújo *et al.*, 2014), since there is a positive correlation between the number of plant species and galling

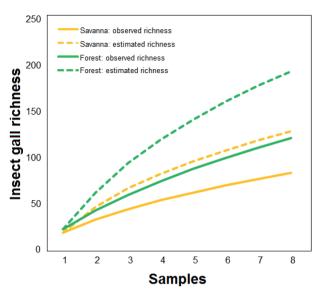


Fig. 6. Sample-based species accumulation curve for insect gall richness observed (continuous lines) and estimated (tracked lines) in the savanna (gray lines) and forest (black lines) habitats of the Flona-Silvânia, Goiás, Brazil.

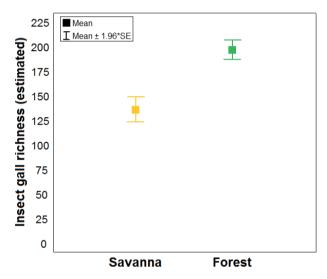


Fig. 7. Comparison of the estimated insect gall richness (1st order Jackknife estimator) between savanna and forest habitats in the Flona-Silvânia, Goiás, Brazil.

species (Araújo, 2011). In the present study, Fabaceae and Asteraceae hosted insect galls mainly in the savanna. In the forest area, alternative host families such as Burseraceae, Siparunaceae and Sapindaceae were more important, hosting together 35.3% of the insect gall diversity in this vegetation. Although these families be few diverse in the Cerrado (Mendonça *et al.*, 2008), their great importance in the present study is related to presence of super-host taxa.

Super-host taxa are plant genera or species that exhibit a high intrinsic diversity of galling insects (Veldtman & McGeoch, 2003; Araújo *et al.*, 2013). Some vegetation types can have an increment in the insect gall richness due to occurrence of few super-hosts because they present a

great number of gall morphospecies (ARAÚJO et al., 2013). Corroborating this idea, we found that the more important host plants in the Flona-Silvânia, Protium heptaphylum (Burseraceae) and Siparuna guianensis (Siparunaceae) that together hosted 14% of the total number of insect gall morphotypes, occurred mainly in the forest habitat (only S. guianensis also occurred in savanna vegetation hosting one gall morphotype). According to ARAÚJO et al. (2013) the occurrence of super-host plant species may produce differences in local patterns of galling richness because they represent keystone resources for galling species along the habitat.

Previous studies in Brazilian savannas indicate that plant species richness is an important predictor of the insect gall distribution (e.g., Gonçalves-Alvim & Fernandes, 2001; ARAÚJO et al., 2013), and may even mediate the effects of soil variables and vegetation structure (ARAÚJO, 2017). This may indicate that differences in the insect gall richness between mesic and xeric habitats are easier to observe when these habitats also have contrasting plant species richness, which was not observed in the present study. Furthermore, our rarefaction analysis demonstrated that insect gall richness was less well-sampled in the forest, since the rarefaction curve did not reached the asymptote (i.e., stabilization in the number of species), than in the savanna habitat. On the other hand, as a smaller number of host plant species hosted a larger number of insect gall morphotypes in the mesic habitat transects, the estimated galling species richness was higher for this vegetation type than for the savanna vegetation. Thus, we believe that future studies that compare the diversity of insect galls between xeric and mesic environments should take into account other vegetation factors, such plant architecture, occurrence of super-host taxa and plant species richness.

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