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Thematic Review

Insect galls on Asteraceae in Brazil: richness, geographic distribution, associated fauna, endemism and economic importance

Ismael Cividini Flor[1], *Alene Ramos Rodrigues*[1], *Sharlene Ascendino Silva*[1], *Barbara Proença*[1] & *Valéria Cid Maia*[1]

[1]*Universidade Federal do Rio de Janeiro Museu Nacional, Rio de Janeiro, RJ, Brasil.*
**Corresponding author: ismaelcflor@gmail.com*

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Abstract: An overview of insect galls on Asteraceae in Brazil is presented. We used the Web of Science database to find publications about insect galls from 1988 to 2020. We analyzed 88 publications and collected data from 51 of those. A total of 487 gall morphotypes were counted on 157 plant species of 42 genera. This value singled out Asteraceae as the richest plant family in number of gall morphotypes in Brazil. Most morphotypes were recorded in the Atlantic Forest (41%) and Cerrado (30.5%), the most surveyed biomes in Brazil. *Baccharis* L. supported the greatest gall richness (43.9%), which could be explained by the hypotheses of geographic area and taxon size. *Baccharis concinna* G.M. Barroso, B. *dracunculifolia* DC. and *B. platypoda* DC. were indicated as superhost species. Most galls were induced on stems (52.2%), a pattern known in Asteraceae for gall-inducing Tephritidae and Chloropidae, and extended in the present study to Cecidomyiidae. Most galls were fusiform (42.5%), which can be related to the highest number of gall on stems. Cecidomyiidae (Diptera) were the most frequent inducers, as observed worldwide. The presence of other dwellers - parasitoids, cecidophages, kleptoparasites, and successors - were reported in 8.8% of the gall morphotypes, being parasitoids the most frequent, as found in other Brazilian publications. Most host plants (58%) are endemic to Brazil, 14% are useful and few are vulnerable or endangered (six and four species, respectively). Due to the high host specificity, the gall-inducers associated with these plants can also be considered either endemic, important, vulnerable and/or endangered, respectively.
Keywords: *Gall-inducing insects; insect-plant interaction; Compositae.*

Galhas de insetos em Asteraceae no Brasil: riqueza, distribuição geográfica, fauna associada, endemismo e importância econômica

Resumo: Um panorama geral das galhas de insetos em Asteraceae no Brasil é apresentado. Usamos a base de dados "Web of Science" para encontrar publicações sobre galhas de insetos de 1988 a 2020. Analisamos 88 publicações no total, porém obtivemos dados de apenas 51. Um total de 487 morfotipos de galhas foi contabilizado em 157 espécies de plantas de 42 gêneros. Este valor indica as Asteraceae como a família botânica mais rica em número de morfotipos de galhas no Brasil. A maioria dos morfotipos foi registrada na Mata Atlântica (41%) e no Cerrado (30.5%), biomas mais investigados no Brasil. *Baccharis* L. suportou a maior riqueza de galhas (43.9%), o que poderia ser explicado pelas hipóteses de área geográfica e tamanho do táxon. *Baccharis concinna* G.M. Barroso, B. *dracunculifolia* DC. E B. *platypoda* DC. foram indicadas como as espécies super hospedeiras. A maioria das galhas foi induzida em caules (52.2%), um padrão conhecido em Asteraceae para Tephritidae e Chloropidae indutores de galhas, e estendido no presente estudo para Cecidomyiidae. A maioria das galhas foi fusiforme (42.5%), o que pode estar relacionado ao maior número de galhas em caule. Os Cecidomyiidae (Diptera) foram os indutores mais frequentes, como no mundo inteiro. A presença de outros ocupantes - parasitoides, cecidófagos, cleptoparasitas e sucessores - foi assinalada em 8.8% dos morfotipos de galhas, sendo os parasitoides os mais frequentes, como em outras publicações no país. A maioria das plantas hospedeiras são endêmicas do Brasil (58%), 14 são úteis e algumas são vulneráveis ou ameaçadas (seis e quatro, respectivamente). Devido à alta especificidade de plantas hospedeiras, os indutores de galhas associados a estas plantas podem ser considerados endêmicos, de importância econômica, vulneráveis e/ou ameaçados, respectivamente.
Palavras-chave: *Insetos indutores de galhas; interação inseto-planta; Compositae.*

Introduction

The Asteraceae family presents the largest number of species recorded in the world, totaling 32,581 species (Willis 2017). This group is found in all continents, except Antarctica, being more common in rural environments than in forests (Anderberg et al. 2007). In Brazil, Asteraceae are the third family in species diversity among Angiosperms and in number of endemisms (BFG 2018) with approximately 289 genera and 2,173 species, of which 71 genera and 1,367 species are endemic (Flora do Brasil 2020), occurring preferentially in open environments, such as savannahs and rupestrian fields (Hind & Miranda 2008).

Insect galls are pathological structures that originate new formations in plant tissues, as a result of mechanical and/or chemical stimulation by insects (Bronner 1992). According to Mani (1964), galls are induced in any part of a plant, both in vegetative and reproductive organs, providing food and shelter for the larva until its adult stage. Although the entomogenous galls occur in any part of the plants, they are most common on leaves and branches (Maia & Siqueira 2020).

Several plants of economic interest are vulnerable to damage by gall-inducing insects, including ornamental, edible, medicinal and pesticidal plants, as well as species used in carpentry, cosmetics, cabinet making, and agroforestry (Maia 2018). Most galling pests have been reported from the Old World and North America, whereas few examples are known from South America, especially in plants of the Asteraceae family.

In the last 30 years, several insect gall inventories in different Brazilian phytophysiognomies have been published (Araújo 2018). Most of them comprise galls on Asteraceae and indicate this family as one of the most important in gall richness. Other families are also important, such as Fabaceae (Santos-Silva & Araújo 2020) and Myrtaceae (Maia 2019). As data are scattered in the literature, the number of host plant species and gall-inducing species are unknown, as well as data on their associated fauna, distribution, endemism, and economic importance.

The main goal of this paper is to present a panoramic view of insect galls on Asteraceae in Brazil. The specific objectives are: (1) to inventory the gall-morphotypes on Asteraceae species in Brazil; (2) register the distribution of the galls phytogeographic domains; (3) determine the most frequent morphotype as well as the most attacked plant organ and the presence or absence of pubescence; (4) provide information about the identification of the inducers and the guilds of associated fauna; (5) obtain information about the origin, endemism, status of conservation, and the economic importance of the host plants and their gall inducing species.

Material and Methods

Insect gall scientific articles sampling Brazilian areas published from 1988 until 2020 were analyzed in order to collect information about insect galls on Asteraceae in Web of Science between August, 2020 and October, 2020 (www.periodicos.capes.gov.br). The following descriptors were used: Brazil/*Brasil*, Galls/*Galhas*, Insect galls/*Galhas de insetos*, Gall-inducing insects/*Insetos galhadores*, Cecidomyiidae, Asteraceae, Compositae. We only considered host plants identified to species level, to avoid overestimating gall morphotypes number.

Botanical names and synonyms were verified in Flora do Brasil (2020), as well as data on plant origin, geographic distribution and conservation categories (EN - endangered, LC - least concern, NE - not evaluated, NT - near threatened, VU - vulnerable) (IUCN 2020). Plant uses were verified using the websites Useful Tropical Plants Database (2014 - http://tropical.theferns.info) and EMBRAPA (https://www.embrapa.br/). The following categories were considered: agroforestry, edible, medicinal and other uses. Phytogeographic domains were retrieved from the original papers or verified in vegetation maps of Brazil (IBGE 2004). Host plants that occur exclusively in one single domain were considered as endemic of this domain. The plant species that presented the highest number of galls were considered galls' super-hosts.

Gall shapes were standardized based on Isaias et al. (2013), whenever possible. When published data were insufficient for standardization, we kept the terminology of the original papers. To establish the number of gall morphotypes per plant species, we compared gall morphology. Whenever we found galls with similar morphological characterization, but listed as different morphotypes in the same paper, we adopted the author(s)' concept.

In the present study, all records of Cecidomyiidae (Diptera) as gall-inducer were converted in Cecidomyiinae records, since this is the single subfamily of Cecidomyiidae which includes cecidogenous species (Gagné & Jaschhof 2021). Concerning the associated fauna, records of inquilines were converted in records of cecidophages and kleptoparasites, according to the criteria proposed by Luz & Mendonça-Júnior (2019).

Results

1. *Inventory of galls*

We found 88 articles reporting insect galls sampled from Brazilian areas: 64 with gall morphotypes on Asteraceae, 51 with identified host plant species and 24 of them without Asteraceae as hosts. Asteraceae species appear as hosts of insect galls in 34 (31%) of these studies, and this family is indicated as one of the super hosts in 21 inventories. They covered five (83%) Brazilian phytogeographic domains, with the Atlantic Forest and Cerrado the most studied, with 33 and 29 inventories, respectively. The surveys totaled 487 insect gall morphotypes in association with 157 species of 42 genera (Figure 1). *Baccharis* L. and *Mikania* Willd. showed the highest number of galled species, 42 (26.7%) and 29 (18.5%), and the greatest richness of galls, 218 (43.9%) and 76 (15.6%) morphotypes, respectively. The super-host plant species were: *Baccharis concinna* G.M.Barroso (n=18 morphotypes; 3.7%), *B. dracunculifoli*a DC. (n=17; 3.5%), *B. platypoda* DC. (n=17; 3.5%), *B. reticulari*a DC. (n=17; 3.5%), *B. retusa* DC. (n=16; 3.3%), *B. minutiflora* Mart. ex Baker. (n=14; 2.9%), *Eremanthus erythropappus* (DC.) MacLeish (n=12; 2.5%) and *Mikania glomerata* Spreng. (n=10; 2.1%) (Supplementary Material).

2. *Gall richness by phytogeographic domains*

The Atlantic Forest was the domain with the highest number of gall morphotypes, 200 (41%), followed by Cerrado with 150 (30.5%), Pampa with five, Pantanal with three and Amazon rainforest with two. Caatinga (dry forest) presented the lowest number of galls, with only one morphotype. Eighty-seven (55%) host plant species were recorded only in the Atlantic Forest, sixty-seven only in the Cerrado (42%), eighty in the Atlantic Forest + Cerrado, one in the Caatinga + Cerrado, and two in the Amazon Forest. Thirty-eight host plant species (24.2%) were more widespread than their galls, 28 were as widespread as their galls and 19 host plant species were reported in phytogeographic domains outside their distribution area according to Flora do Brasil (2020) (Table 1), showing that there is still no data on galls for Brazil.

3. Gall morphotypes

Thirteen distinct gall shapes were found, the most frequent were fusiform (42.5%) and globoid (35.1%) (Figures 1 and 2). The shape of two gall morphotypes was not informed. The most attacked organs were stems (n=254; 52.2%), leaves (n=165; 33.9%), bud galls (n=92; 14.2%) and flower (n=14; 2.8%) (Table 2). Galls on flowers (1.3%) were found only in Atlantic Forest and Cerrado. The majority of the galls were glabrous (58.4%), except in Pantanal where among the three galls found, two presented trichomes. Data on pubescence in 28.2% of the morphotypes (n=102) were not informed by the authors as well as the phytogeographic domains of 132 gall morphotypes. In addition, some of the galls occurred simultaneously in more than one plant organ so that the results shown in table 3 have totals higher than the overall number.

4. Gall-inducing insects and associated fauna

The inducers belong to four orders: Diptera (64.7%), Lepidoptera (6%), Hemiptera (3.3%) and Coleoptera (2%). Furthermore, inducers of 117 gall morphotypes (24%) were not determined (Table 3). Two families represented Diptera: Cecidomyiidae (61.8%) and Tephritidae (2.9%). Fifteen genera of gall midges have been recorded, most of

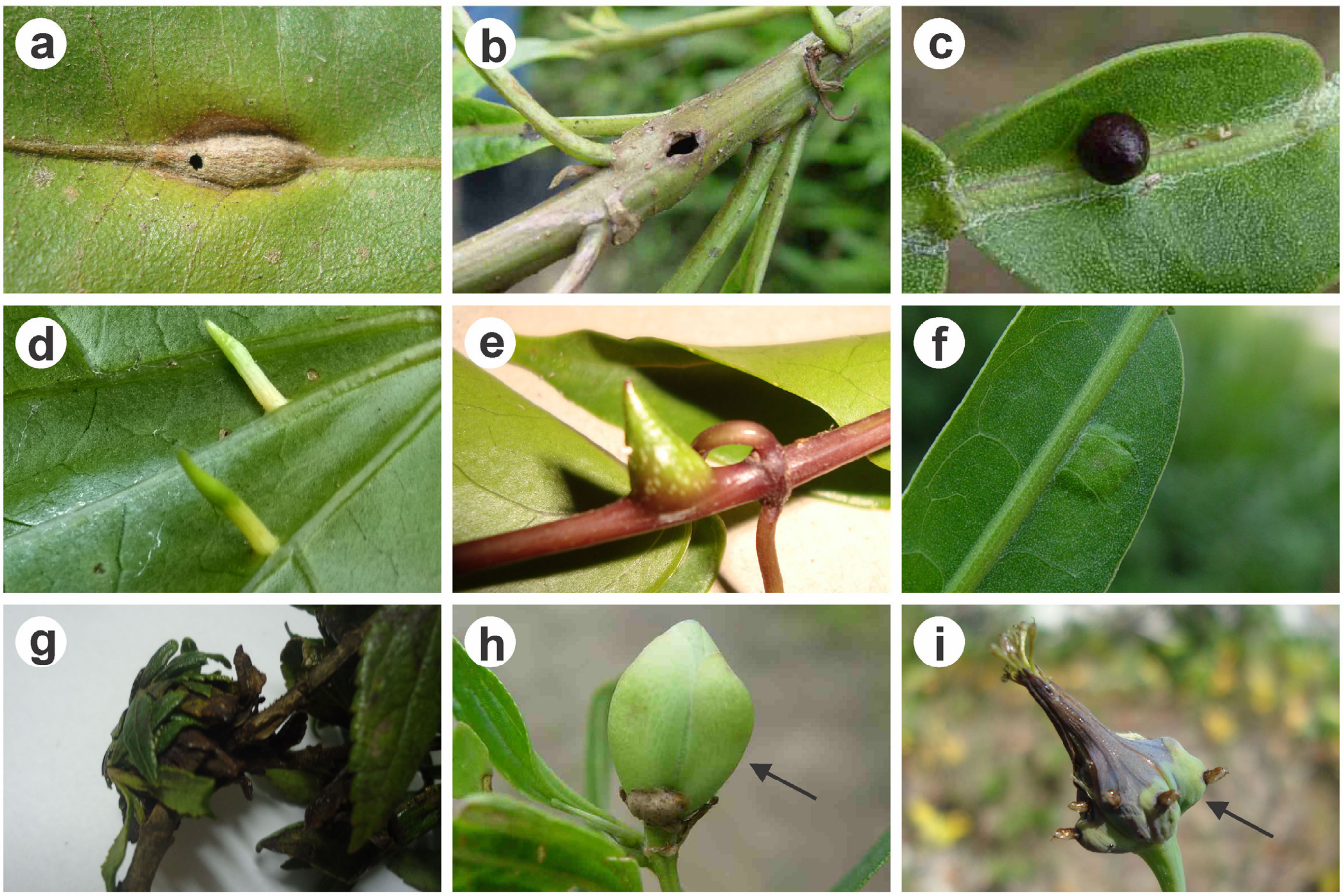

Figure 1. Galls on Asteraceae in Brazil. a) fusiform gall on leaf of *Mikania argyreiae* DC.; b) fusiform gall on stem of *Vernonia beyrichii* Less.; c) globoid gall on leaf of *Baccharis conyzoides* (Less.) DC.; d) cylindrical gall on leaf of *Mikania glomerata* Spreng.; e) conical gall on stem of *Mikania micrantha* Kunth; f) lenticular gall on leaf of *Baccharis conyzoides* (Less.) DC.; g) rosette gall on lateral bud of *Grazielia gaudichaudiana* (DC.) R.M.King & H.Rob.; h) globoid gall on apical bud of *Baccharis dracunculifolia* DC.; and i) fusiform gall with pupal exuvia on Flower-head of *Porophyllum ruderale* (Jacq.) Cass.

Table 1. Number of gall morphotypes by genera and species of Asteraceae, and the average number of gall per host plant species in each phytogeographic domain in Brazil.

Phytogeographic domain	Nº of galled plant genera	Nº of host species	Nº of morphotypes	Average number of gall/ host plant species
Atlantic Forest	29	87	200	2.3
Amazon	02	02	02	1.0
Caatinga-Cerrado	01	01	01	1.0
Cerrado	26	67	150	2.2
Pampa	03	04	05	1.25
Pantanal	02	02	03	1.5
No data	05	13	139	-

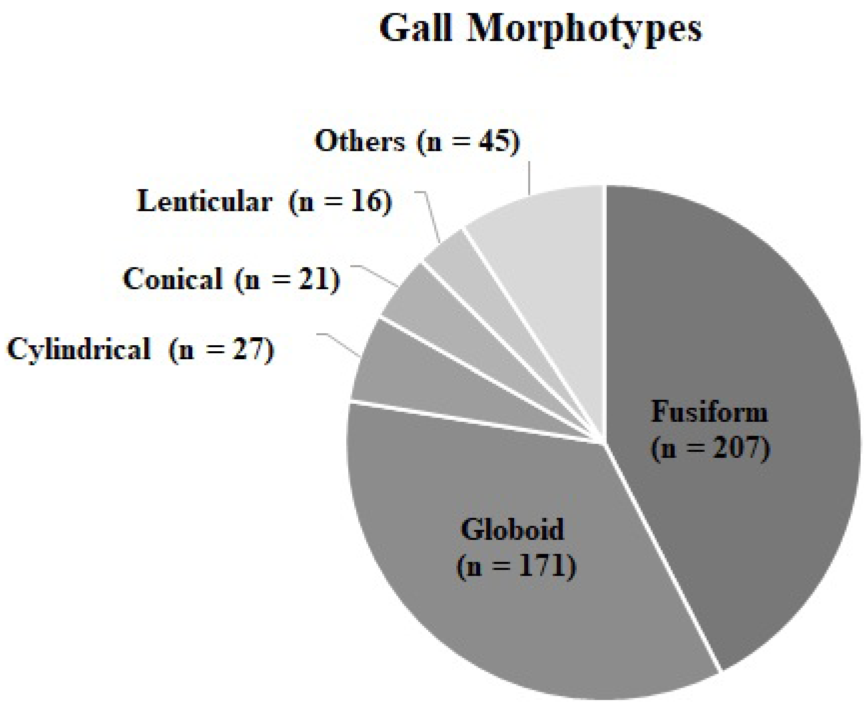

Figure 2. Number of gall morphotypes recorded on Asteraceae species in Brazil. Other morphotypes: rosette, marginal roll, amorphous, discoid*, claviform, ovoid*, spherical*, swelling* and not informed (* morphotypes with terminology not updated).

Table 2. Number of gall morphotypes per plant organ of Asteraceae species in each phytogeographic domain in Brazil.

Plant organs	Atlantic Forest	Cerrado	Pantanal	Pampa	Amazon	Caatinga-Cerrado
Stem	92	89	2	3	1	1
Leaf	84	51	1	2	1	-
Bud	35	20	-	-	-	-
Flower	3	2	-	-	-	-

them (n=12) are represented by a single identified species, except *Asphondylia* (n=4 species), *Liodiplosis* (n=3), and *Clinodiplosis* (n=2). Furthermore, nine genera include undetermined species, highlighting *Asphondylia* due to its highest richness. Tephritidae were registered in 14 gall morphotypes, with only one inducer identified in species, *Tomoplagia rudolphi* (Lutz & Lima, 1918) on *Vernonanthura polyanthes* (Sprengel) Vega & Dematteis.

Associated fauna were found in 43 gall morphotypes (8.8%) on 30 plant species of 15 genera (Table 4). *Mikania* and *Baccharis* comprised the highest number of morphotypes with associated fauna (14 and 9, respectively). Four guilds were represented: cecidophages, kleptoparasites, parasitoids, and successors. Among them, parasitoids were the most frequent, found in 29 gall morphotypes on 24 plant species, followed by cecidophages, found in 12 gall morphotypes on 11 plant species, and kleptoparasites in eight morphotypes on three plant species. Successors were the least frequent, being found in six gall morphotypes on six plant species.

Parasitoids were represented by Hymenoptera of six families, the most frequent being Eulophidae (n=9) and Eurytomidae (n=4). Multiparasitism was reported in six gall morphotypes. Cecidophages were represented by Diptera, Hemiptera, Coleoptera, Lepidoptera, and Thysanoptera. Diptera were the most frequent being found in seven gall morphotypes followed by Coleoptera (n=4), Lepidoptera (n=3), Hemiptera (n=2), and Thysanoptera (n=2). Kleptoparasites were represented by Cecidomyiidae (Diptera), while successors by Formicidae (Hymenoptera) and Collembola. Spiders were recorded in a single gall morphotype, but the authors did not include these organisms in any guild (Silva et al. 2018).

The four guilds were reported only in Atlantic Forest, while only kleptoparasites were not recorded in the Cerrado. In the Caatinga-Cerrado transition and Amazon Forest only one guild was reported, successors and kleptoparasites, respectively. Thirty gall morphotypes hosted associated fauna in the Atlantic Forest, 11 in the Cerrado, one in Amazon Forest, and one in the Caatinga-Cerrado transition.

Table 3. Richness of gall morphotypes per order and family of inducing insects.

Inducers		Number of gall morphotypes	%
Order	**Family**		
Diptera	Cecidomyiidae	301	61.8
	Tephritidae	14	2.9
Coleoptera		06	1.2
	Curculionidae	04	0.8
Hemiptera		05	1.0
	Psyllidae	11	2.3
Lepidoptera		29	6.0
Not determined		117	24.0

Table 4. Associated fauna of galls on Asteraceae species and their phytogeographic domains of occurrence. (1) Cecidophages, (2) Parasitoids, (3) Kleptoparasites, (4) Successors, (5) not determined guild.

Host plant species	Gall morphotypes	Associated fauna	Phytogeographic domains
Ageratum conyzoides L.	Bud / globoid	Aphidae (Hemiptera) (1) Muscomorpha (Diptera) (1)	Atlantic Forest
Baccharis bifrons Baker	Leaf / lenticular	Hymenoptera (2)	Atlantic Forest
Baccharis microcephala (Less.) DC.	Bud / globoid	Eulophidae (Hymenoptera) (2) *Galeopsomyia sp*. (Eulophidae) (2) *Eurytomasp.* (Eurytomidae, Hymenoptera) (2)	Atlantic Forest
	Leaf mid vein / fusiform	Eulophidae (Hymenoptera) (2) *Galeopsomyia* sp. (Eulophidae) (2) *Eurytoma* sp. (Eurytomidae, Hymenoptera) (2)	
Baccharis pedunculata (Mill.) Cabrera	Bud and stem / fusiform	Lepidoptera (1) Collembola (4) Platygastridae (Hymenoptera) (2)	Atlantic Forest
Baccharis pingraea (Lam.) Pers	Stem and leaf / globoid	Hymenoptera (2)	Cerrado
Baccharis reticularia DC.	Bud and stem / globoid	Sciaridae (Diptera) (1) Formicidae (Hymenoptera) (4)	Cerrado
	Leaf / marginal roll	Heteroptera (Hemiptera) (1)	
	Leaf petiole, leaf vein and stem / fusiform	Platygastridae (2)	
Baccharis singularis (Vell.) G. M. Barroso	Leaf vein and stem / fusiform	Thysanoptera (1)	Atlantic Forest
Calea pinnatifida (R. Br.) Less	Stem / fusiform	Hymenoptera (2)	Atlantic Forest
Chromolaena odorata (L.) R.M.King and H.Rob.	Stem / conical	*Trotteria lapalmae* Möhn, 1975 (Cecidomyiidae, Diptera) (3)	Amazon Forest
	Leaf vein / fusiform	Hymenoptera (2)	Atlantic Forest
Eremanthus capitatus (Spreng.) MacLeish	Stem / globoid	Formicidae (4)	Caatinga-Cerrado
Eremanthus polycephalus (DC.) MacLeish.	Stem / globoid	Formicidae (4)	Atlantic Forest
Graphistylis itatiaiae (Dusén) B.Nord.	Bud / fusiform	Hymenoptera (2)	Atlantic Forest
Grazielia gaudichaudeana (DC.) R.M.King and H.Rob.	Leaf / globoid	Lepidoptera (1)	Atlantic Forest
Lepidaploa rufogrisea	Stem / globoid	Sciaridae (1) Resseliella sp. (Cecidomyiidae) (3) Hymenoptera (2)	Atlantic Forest
Mikania argyreiae DC.	Leaf / globoid	Hymenoptera (2)	Atlantic Forest
Mikania glomerata Spreng.	Stem / conical	*Contarinia ubiquita* Gagné, 2001 (Cecidomyiidae) (3)	Atlantic Forest
	Leaf / globoid	*Contarinia* sp. (Cecidomyiidae) (3) *Clinodiplosis* sp. (Cecidomyiidae) (3) Coleoptera (1) Hymenoptera (2) Thysanoptera (4)	

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	Leaf / cylindrical	Hymenoptera (2)	
	Leaf petiole / fusiform	*Contarinia ubiquita* (3)	
	Stem / fusiform	*Clinodiplosis* sp. (3)	
	Bud / globoid	*Contarinia ubiquita* (3)	
Mikania hoehnei Robinson	Leaf / marginal roll	Hymenoptera (2) Eulophidae (2) Sciaridae (1)	Atlantic Forest
	Stem / globoid	*Dimeromicrus cecidomyiae* (Ashmead, 1887) (Torymidae, Hymenoptera) (2)	
Mikania involucrata Hook. &Arn.	Stem / amorphous	Torymidae (2)	Atlantic Forest
Mikania lasiandra DC.	Leaf and stem / globoid	Hymenoptera (2)	Atlantic Forest
Mikania lindbergii Baker	Stem / fusiform	Hymenoptera (2)	Cerrado
Mikania periplocifolia Hook. andArn.	Leaf vein / fusiform	Hymenoptera (2)	Atlantic Forest
Mikania pseudohoffmanniana G. M. Barroso	Stem / fusiform	Hymenoptera (2)	Atlantic Forest
Moquiniastrum paniculatum (Less.) G. Sancho	Leaf / globoid	Eulophidae (2) Eurytomidae (2)	Atlantic Forest Cerrado
Moquiniastrum pulchrum (Cabrera) G.Sancho	Leaf and bud / amorphous	Eulophidae (2)	Cerrado
Porophyllum ruderale (Jack.) Cass.	Stem / fusiform	Eulophidae (2) Eurytomidae (2)	Atlantic Forest Cerrado
	Inflorescence / fusiform	*Trypanea* sp. (Tephritidae, Diptera) (1)	Atlantic Forest
Pterocaulon virgatum (L.) DC.	Stem / globoid	Hymenoptera (2)	Atlantic Forest
Symphyopappus reticulatus Baker	Stem and leaf vein / fusiform	Muscomorpha cfr. (1) Hymenoptera (2)	Atlantic Forest
Verbesina macrophylla(Cass.) S.F.Blake	Bud / globoid	Araneae (5) Lepidoptera (5)	Cerrado
Vernonanthura beyrichii (Less.) H.Rob.	Bud and stem / fusiform	Sciaridae (1) Lepidoptera (1) Collembola (4)	Atlantic Forest
Vernonanthura membranacea (Gardner) H.Rob.	Bud / globoid	Hymenoptera (2)	Atlantic Forest
Vernonanthura polyanthes (Spreng) Vega & Dematteis	Stem and leaf bud / globoid and fusiform,	Braconidae (2) (Hymenoptera) Eulophidae (2)	Cerrado
	Leaf and stem / globoid	Torymidae (2) Chalcididae (2) (Hymenoptera)	Atlantic Forest Cerrado

5. *Origin, endemism and economical importance*

Regarding the origin of the host plant species, 96.8% (n=152) are native to Brazil, among them 58% (n=91) are endemic to Brazil, 25.3% (n=23) being endemic to the Atlantic Forest, 30.8% to Cerrado and 1.1% to Caatinga (Table 5). *Chromolaena ivifolia* (L.) R.M.King & Lamp; H.Rob. and *Mikania lindleyana* DC. were recorded in the Amazon rainforest and *Aspilia latissima* Malme and *Vernonanthura brasiliana* (L.) H.Rob. in the Pantanal, species that are native but not endemic. There was no occurrence of Asteraceae in the Caatinga, but one species was recorded in a transition area between Caatinga to Cerrado.

Concerning IUNC (2020) conservation categories, plant species were classified into: NE: 79.6% (n=125 plants; 392 morphotypes), LC: 7.6% (n=12; 43), NT: 4.5% (n=7; 13), VU: 3.8% (n=6; 30) and EN: 2.5% (n=4; 6). The Cerrado presented the largest number of threatened species (EN, NT and VU), 13, followed by the Atlantic Forest biomes with four (VU).

Among the 157 host plants, only 22 (14%) are economically useful, most being medicinal (59%), 36.3% have agroforestry use and only 18.8% are edible. Furthermore, 54.5% have other uses (Table 6). These plants host 98 gall inducing insects, most of them are Cecidomyiinae (65.3%), followed by Tephritidae (7.1%), Hemiptera (5.1%), Lepidoptera (4%) and Coleoptera (2%). In 16.3% the galling insects were not determined. Eighteen inducers were identified at species level and six at genera level.

Discussion

In this study we compiled 487 gall morphotypes on Asteraceae, a higher number than compiled on Fabaceae (n=437) by Santos-Silva & Araújo (2020), showing that Asteraceae are the main insect gall hosts in Brazil. Nevertheless, the number of galled species is higher in Fabaceae (n=178) than in Asteraceae (n=157). Although the Cerrado has the largest number of Asteraceae species (n=1,238) (Flora do Brasil 2020), the Atlantic Forest presents the highest number of galled plant species, gall morphotypes and articles reporting galls. In a similar study with Fabaceae, Santos-Silva & Araújo (2020) reported the greatest gall richness in the Cerrado, while the Atlantic Forest occupied the second place. The highest gall richness of Atlantic Forest and Cerrado can be explained by the fact that these biomes have been more intensely surveyed and additionally they housed the first research centers focusing on gall-inducing insects in Brazil (Universidade Federal de Minas Gerais and Universidade Federal do Rio de Janeiro, respectively) (Araújo et al. 2019).

Table 5. Origin of Asteraceae host species and number of gall morphotypes in Brazil.

Origin	**Number of host plants**	**Number of galls**
Native	152	482
No data	05	05
Total	**157**	**487**
Endemic to Brazil	39	145
Endemic to Atlantic Forest	23	50
Endemic to Cerrado	28	74
Endemic to Caatinga	01	01
Not Endemic	59	205
No data	07	12
Total	**157**	**487**

Table 6. The Asteraceae species hosting insect galls in Brazil, their economic importance, and the number of gall inducer morphospecies by host plant.

Host Plant	**Economic Importance**				**Number of gall inducer morphospecies**
	Medicinal	**Edible uses**	**Agroforestry**	**Other uses**	
Achyrocline satureioides (Lam.) DC	x	-	-	-	01
Ageratum conyzoides L.	x	x	-	x	05
Aspilia foliosa (Gardner) Benth. & Hook.	x	-	-	-	02
Austroeupatorium inulaefolium (Kunth) R.M.King&H.Rob.	-	-	x	-	01
Baccharis dracunculifolia DC.	-	-	-	x	17
Baccharis reticularia DC.	-	-	-	x	17
Chromolaena odorata (L.) R.M.King and H.Rob.	x	x	x	x	05
Conyza canadensis (L.) Cronquist	x	x	x	x	01
Dasyphyllum brasiliense (Spreng.) Cabrera	-	-	-	x	02
Dasyphyllum spinescens (Less.) Cabrera	-	-	x	x	03
Eremanthus erythropappus (DC.) MacLeish	-	-	x	x	08
Lychnophora ericoides Mart.	x	-	-	-	02
Lychnophora pinaster Mart.	x	-	-	-	02
Mikania glomerata Spreng.	x	-	-	-	10
Mikania laevigata Sch.Bip. ex Baker	x	-	-	-	03
Mikania micrantha Kunth	x	-	x	-	08
Piptocarpha axillaris (Less.) Baker	-	-	-	x	01
Piptocarpha rotundifolia (Less.) Baker	x	-	x	x	02
Porophyllum ruderale (Jack.) Cass.	x	x	-	x	01
Pseudobrickellia brasiliensis (Spreng.) R.M.King	x	-	-	-	01
Vernonanthura brasiliana (L.) H.Rob.	-	-	-	x	02
Vernonanthura polyanthes (Sprengel) Vega & Dematteis	-	-	x	-	04

The genera with the largest number of galled species and gall morphotypes were *Baccharis* and *Mikania*. A large number of galls induced by insects have been studied on many species of *Baccharis* and *Mikania* (Fernandes et al. 2014). Both these genera are widely distributed throughout Brazil and they are the richer in species within the Asteraceae family, favoring their association with gall-inducing insects. The hypothesis of geographic area (Southwood 1960) and hypothesis of taxon size (Fernandes 1992) could perhaps help explain the greater insect galls richness on *Baccharis* and *Mikania*. They predict that taxa with wider geographic distribution and greater species richness have potentially a greater number of associated galling insects than taxa with more restricted distribution and lower species richness. The presence of super-hosts species is common in the Neotropical region; hence contributing to the increase of the local and regional fauna of gall-inducers in the communities (Fernandes et al. 2014). *Baccharis dracunculifolia* and *B. concinna* were also reported by Fernandes et al. (1996) as super-hosts, as well as *Mikania glomerata* in different inventories in Brazil (Maia 2013, Maia & Proença 2016).

The highest frequency of the fusiform galls in this study differs from the pattern observed in the Neotropical region where conical galls are the most common (Isaias et al. 2014). Santos-Silva & Araújo (2020) reported a predominance of globoid galls in Fabaceae. The highest number of fusiform galls in our study can be related to the high number of gall on stems. When compared to leaves, stems are less plastic organs, perhaps not allowing many variations in the gall shape (Valladares et al. 2006). The predominance of stem galls differ from the pattern of all zoogeographic regions, where most galls are on leaves (Mani, 1964). However, the higher number of stem galls in Asteraceae is a pattern already known for some gall-inducing taxa, as Tephritidae (Friedberg 1984), Chloropidae (Foote et al. 1993), and Lepidoptera (Maia 2006). In the present study, the last pattern is suggested for gall midges too.

Cecidomyiidae were the most frequent gall-inducers. In fact, they represent the most diverse gall-inducing family in the whole world. They comprise about 6,590 species, about 70% of them being gall-inducing (Gagné & Jaschhof 2021). The *Asphondylia* was the most diverse gall-inducing genus in our study. This genus is speciose, cosmopolitan and easily recognizable and these features could explain its richness (Gagné & Jaschhof 2021). Other Diptera families include gall-inducers, as Tephritidae, but in this family, only a small percentage of species (about 10%) exhibits this habit. Nevertheless, most Tephritidae species induce galls on Asteraceae and this is recognised as a worldwide pattern (Freidberg 1984). Most described species of Cecidomyiidae induce galls on Myrtaceae in Brazil (Maia 2019). Galls of Lepidoptera, Coleoptera and Hemiptera are less frequent than those of Cecidomyiidae, nevertheless, these orders are frequently reported (*e.g.* Gonçalves-Alvim & Fernandes 2001, Maia et al. 2008, Malves & Frieiro-Costa 2012), but always responsible for few gall morphotypes.

In this study parasitoids were the most frequent guild as in several Brazilian inventories, being represented exclusively by Hymenoptera (*e.g.* Carvalho & Mota 2018, Silva et al. 2018, Maia & Siqueira 2020). In fact, they are considered the most important natural enemies of the gall-inducing insects, not only in Brazil, but also in the world (Gagné 1994). Eulophidae and Eurytomidae are families usually cited as parasitoids of gall-inducers in Brazil (*e.g.* Maia 2001, Carvalho-Fernandes et al. 2016, Ribeiro et al. 2019). Cecidophages, kleptoparasites and successors are infrequent in inventories, and the insect taxa included in these guilds have been found in Asteraceae as well as in other plant families (*e.g.* Maia 2001, Carvalho-Fernandes et al. 2016, Maia & Siqueira 2020).

Few studies refer to the origin, endemism and threat category of host plant species associated with galling insects. Among the 88 scientific publications studied, only three presented this information (Maia & Mascarenhas 2017, Maia & Siqueira 2020, Santos-Silva & Araújo 2020). In our study 50% are endemic and this value is higher when compared to that of Santos-Silva & Araújo (2020) for Fabaceae (29%). Furthermore, 17 botanical species are under a threatened category of conservation. Given the accepted high levels of host-inducer specificity (Carneiro et al. 2009), we suggest that gall inducers associated exclusively with endemic hosts are endemic and those associated with threatened plants are also threatened.

Despite the low percentage of useful plants observed in this study, it is important to quantify the diversity of gall inducers, because their presence can cause several damage, such as, plant growth reduction, lower photosynthesis rate and reduced fruits, resulting in economic losses (McCrea et al. 1985, Fernandes 1987, Souza et al. 1998). These losses can be increased when more than one galling species occur on the same host, as we observed in 77.2% of the useful species of Asteraceae. Once again, based on species-specificity, we suggest that all Cecidomyiidae related to useful plants can be considered at least potentially of economic importance.

Conclusions

We can conclude that Asteraceae is the main host family of insect galls in Brazil and most morphotypes were reported in the Atlantic Forest and Cerrado. The richest genera in gall morphotypes were also the most widely distributed around Brazil and one of the best represented in number of species. The most attacked plant organ and the most frequent gall morphotype on Asteraceae do not corroborate the pattern observed for the Neotropical region.

The composition of gall inducing insects and fauna associated followed what is already known for the Neotropical region. Due to Cecidomyiidae high level of specificity, they can be considered endemic, useful, vulnerable and/or threatened as well as their host plants.

Finally, this study provides important data on the presence of gall inducing insects in one of the richest families of Angiosperms in Brazil. Such studies are rare in Brazil important to consolidate the current knowledge, and to show the diversity and frequency of these insects in Brazil. They also provide subsidies to other studies such as biogeography and conservation.

Supplementary Material

The following online material is available for this article:
Table - Insect galls on Asteraceae species occurring in Brazil.

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Gustavo Graciolli

Author Contributions

Ismael Cividini Flor: Conceptualization (Equal), Data curation (Equal), Investigation (Equal), Methodology (Equal), Project administration (Equal), Resources (Equal) Supervision (Equal), Writing – original draft (Equal), Writing – review & editing (Equal).

Alene Ramos Rodrigues: Conceptualization (Equal), Data curation (Equal), Investigation (Equal), Methodology (Equal), Writing – original draft (Equal), Writing – review & editing (Equal).

Sharlene Ascendino Silva: Conceptualization (Equal), Data curation (Equal), Investigation (Equal), Methodology (Equal), Writing – original draft (Equal), Writing – review & editing (Equal).

Barbara Proença: Conceptualization (Equal), Data curation (Equal), Investigation (Equal), Methodology (Equal), Writing – original draft (Equal), Writing – review & editing (Equal).

Valéria Cid Maia: Conceptualization (Equal), Data curation (Equal), Investigation (Equal), Methodology (Equal), Supervision (Equal), Writing – original draft (Equal), Writing – review & editing (Equal).

Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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