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BIOLOGICAL SCIENCES

Are Fabaceae the principal super-hosts of galls in Brazil?

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Abstract: We surveyed 58 scientific articles published between 1987 and 2018 to evaluate the representative nature of the Fabaceae as hosts of insect galls in Brazil, and to gain a better understanding of the interactions between gall-inducing insects and plants and the evolutionary ecology of those insects and their plant hosts. A total of 438 gall morphotypes were reported as being generated by gall-inducing insects on 178 Fabaceae host species belonging to five subfamilies Caesalpinioideae (22 genera and 79 spp.), Cercidoideae (1 genus and 11 spp.), Detarioideae (6 genera and 17 spp.), Dialioideae (2 genera and 2 spp.), and Papilionoideae (26 genera and 69 spp.). The plant host genera demonstrating the greatest richness of gall-inducing insects were *Inga*, *Bauhinia*, and *Copaifera*; the super-host species were *Copaifera langsdorffii*, *Bauhinia brevipes*, and *Copaifera sabulicola*. Most of the galls were observed on leaves; they were mostly globoid, green, glabrous, isolated, and unilocular. The principal gall inducers belonged to Cecidomyiidae; the associated fauna was represented by Collembola, Coleoptera, Diptera, Formicidae, Hemiptera, Hymenoptera, Lepidoptera, Pseudoscorpionida, and Thysanoptera. Fabaceae are the principal super-hosts of galls and one of the most diverse families of angiosperms in Brazil, aggregating evidences for the hypotheses of floristic richness and taxon size.

Key words: Cecidomyiidae, cerrado, insect-plants interactions, Leguminosae, super-host.

INTRODUCTION

Galls are complex structures that develop through interactions between host plants and inducing organisms. Plant cells may undergo hypertrophy due to abnormal differentiation in response to both mechanical and chemical inductors, resulting in the characteristic growths that shelter gall-inducing insects (Raman 2007). Different groups of organisms can induce galls, including acarids, nematodes, and fungi, although insects are the most frequent group (Mani 1964).

Insect gall-inducers generally demonstrate greater degrees of host specificity than most other phytophagous taxa (Carneiro et al. 2009). When a given gall-inducing insect interacts with more than one plant species, those plants are generally phylogenetically closely related species (Bourg & Hanson 2014).

Gall diversity is intimately linked to plant diversity (Wright & Samways 1998, Cuevas-Reyes et al. 2004), and greater numbers of plant species in a given environment create more ecological niches to be exploited (Wright & Samways 1998, Cuevas-Reyes et al. 2004, Mendonça Júnior 2007). Additionally, plant families (or genera) with greater numbers of species will host greater richnesses of gall-inducing insects than plant taxa with smaller numbers of species (Gonçalves-Alvim & Fernandes 2001, Veldtman & Mcgeoch 2003). Plant taxa that host the greatest

numbers of associated gall-inducing insects are known as super-hosts (Fernandes & Price 1988, Veldtman & Mcgeoch 2003, Espírito-Santo & Fernandes 2007). In spite of a general consensus concerning the existence of plant groups that are more susceptible to gall induction, the ecological mechanisms and selective pressures which influence that pattern have yet to be sufficiently explained.

Among the plant families with the greatest richness of host species in the neotropical region is Fabaceae (Leguminosae) (Gagné 1994). Fabaceae represent the third-largest angiosperm family, with 770 genera and approximately 19,500 species distributed among the subfamilies Caesalpinioideae, Cercidoideae, Detarioideae, Dialioideae, Duparquetioideae, and Papilionoideae (LPWG 2013, 2017). The Fabaceae comprise also the largest plant family in Brazil, with wide distribution and an estimated 2,834 species distributed throughout the Amazon Forest, Atlantic Forest, Caatinga, Cerrado, Pampa, and Pantanal phytogeographical domain (BFG 2015).

The Fabaceae are among the most highly valued plants throughout the world (Queiroz 2009, LPWG 2017). They are sources of human foods (*e.g.*, *Phaseolus vulgaris* L.); and popular folk medicines (*e.g.*, *Glycyrrhiza glabra* L.); they serve as forage plants (*e.g.*, *Medicago sativa* L.); and they provide wood (*e.g.*, *Dalbergia nigra* [Vell.] Alemão ex Benth.), oils (*e.g.*, *Arachis hypogaea* L.), resins (*e.g.*, *Copaifera multijuga* Hayne), and dyes (*e.g.*, *Glycine max* [L.] Merril) (Polhill & Raven 1981, Lima et al. 1994).

In spite of the floristic importance of the Fabaceae and their roles as hosts for galling inducers, information concerning the diversity and distribution of those insects and their association with their host species is scattered in the scientific literature. Only a single publication has dealt with gall diversity and associations with plant host species in the Serra Geral Mountains in Caetité, Bahia State, Brazil (Costa et al. 2014a). The present study therefore seeks to evaluate the representative nature of Fabaceae as hosts to galls in Brazil, contribute to our taxonomic knowledge of the inducer species and their respective plant hosts, update data concerning the geographic distributions of those plants in Brazil, and provide subsidies for future biological and ecological studies on those themes.

MATERIALS AND METHODS

The occurrence of galls associated with Fabaceae was verified by consulting the Portal de Periódicos da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (Capes), ProQuest, SciELO, Scopus, SPELL, and Springer Science databases, as well as Google Scholar (http://scholar.google.com.br), during the period between August/2017 and July/2018, utilizing the following descriptors: Brazil, Cecidomyiidae, Galls, Fabaceae, and Leguminosae. Only papers published in the period from 1987 to 2018 were considered, because the gall studies became more frequent in Brazil in the early the 1980s (Moreira 2006). Undergraduate theses or dissertations were not included in the searches due to the difficulty of encountering fully work.

The articles were organized according to their year of publication and journal, and subsequently classified according to topic (the area(s) of knowledge they best matched) – plant anatomy, ecology, taxonomy and inventory – based on their title and abstract to consider only articles appropriate to the scope of the present research.

To avoid over-counting of the gall morphotypes and their host plant, only gall records that reported the host species were

considered; those records that reported only the family, subfamily or genus of host plant were not. The informations about morphotypes found in the compiled papers were standardized following the terminology proposed by Isaias et al. 2013.

The plant taxa were organized alphabetically based on their Fabaceae subfamilies, genera, and species, following the legume LPWG classification system (LPWG 2017). The correct orthography and authors' names were confirmed by consulting the International Plant Name Index (https://www.ipni.org/). The numbers of Fabaceae species per phytogeographical domain and those of the other most diverse angiosperm families in Brazil were obtained by consulting the Flora do Brasil 2020 site (http://reflora.jbrj.gov.br) and the Brazil Flora Group (BFG 2015), respectively. Plant host and morphotype record for more than one vegetation or transition area were counted in each vegetation involved.

RESULTS

A total of 268 articles were published in the scientific literature between 1987 and 2018 concerning the occurrence of galls associated with Fabaceae, of which 58 focused on Brazil. Those articles were published in 26 different scientific periodicals, principally the Biota Neotropica (18.9%), Revista Brasileira de Entomologia (15.5%), and Brazilian Journal of Biology (6.8%); they are listed in Table I.

The first records of insect galls induced on Fabaceae hosts were published by the naturalist Joaquim da Silva Tavares between 1905 and 1925 (Table II). There were significant increases in the numbers of published records after that, especially in the years after 2,000. Current knowledge concerning gall-inducing insects associated with Fabaceae is based on a variety of approaches focusing on plant anatomy (the anatomy and histochemistry of galls), ecology (investigations of ecological factors at the population level), taxonomy (systematics and descriptions of gall-inducing species), and primarily inventories (checklists of gall inducers and their plant hosts) (Table I).

A total of 438 distinct gall morphotypes hosting gall-inducing insects have been recorded in Brazil among 178 species of Fabaceae belonging to five subfamilies: Caesalpinioideae (22 genera and 79 spp.), Cercidoideae (1 genus and 11 spp.), Detarioideae (6 genera and 17 spp.), Dialioideae (2 genera and 2 spp.), and Papilionoideae (26 genera, and 69 spp.) (Table SI- Supplementary Material, Figs 1, 2).

The subfamilies Caesalpinioideae (n=174), Papilionoideae (n=121), and Detarioideae (n=76) hosted the largest numbers of gall types. *Inga* Mill. (Caesalpinioideae), *Machaerium* Pers. (Papilionioideae), and *Bauhinia* L. (Cercidoideae) were the genera demonstrating the greatest host species richness (25, 13, and 11 species, respectively). The plant genera with the greatest richness of galls were *Inga*, *Bauhinia*, *Copaifera* L. (72, 62, 51 morphotypes, respectively) (Table SI). The super-host plant species were: *Copaifera langsdorffii* Desf. (n=28, Figure 2), *Bauhinia brevipes* Vogel (n=17), and *Copaifera sabulicola* J. A. S. Costa & L. P. Queiroz (n=12, Figure 2).

Of the 178 gall-hosting Fabaceae species in this study, 53 are endemic to Brazil, where they occur in all of the country's phytogeographical domains (Table SI). The greatest richness of galls and host species taxa were observed in the Cerrado phytogeographical domain (n=196 morphotypes/n= 59 spp.), followed by the Atlantic forest (n=89/n=47) and Amazon forest (n= 73/n= 44) (Table III).

The plant organ having the most galls was the leaf (n=306; with galls appearing on both

the adaxial and abaxial faces), followed by the stem (n=102). Most of the gall morphotypes were globoid (32%) (Table IV), green (45%), glabrous (81%), isolated (78%), and contained only a single larval chamber (80%) (Table SI).

The gall-inducing insects identified belonged to the orders Diptera (n= 252), Hymenoptera (n=16), Coleoptera (n=11), Lepidoptera (n=7), Hemiptera (n=5), Acari (n=1), and Thysanoptera (n=1), with Cecidomyiidae (Diptera) being responsible for inducing the most varied gall morphotypes (n= 252) (Table SI). The insect fauna associated with the galls included representatives of the Hymenoptera (n=74), Coleoptera (n=3), Hemiptera (n=3), Collembola (n=2), Lepidoptera (n=2), Thysanoptera (n=2), Diptera (n=1), Formicidae (n=1), and Pseudoscorpionida (n=1) (Table SI).

Table I. Articles concerning galls induced in Leguminosae in Brazil that were published in scientific journals between 1987 and 2018 and indexed on the Portal Platform of Periodicals CAPES (www.periodicos.capes.gov.br)

N	Author	Title	Year	Journal
1	Fernandes et al.	Food web relationships involving *Anadiplosis* sp. galls (Diptera: Cecidomyiidae) on *Machaerium auleatum* (Leguminosae).	1987	Revista Brasileira de Botânica
2	Fernandes et al.	Ocorrência e caracterização de galhas entomógenas na vegetação de Campus da Pampulha na Universidade Federal de Minas Gerais	1988	Revista Brasileira de Zoologia
3	Fernandes et al.	Insect galls from savanna and rocky fields of the Jequitinhonha Valley, Minas Gerais, Brazil	1997	Naturalia
4	Gonçalves-Alvim & Fernandes	Comunidades de insetos galhadores (Insecta) em diferentes fitofisionomias do cerrado em Minas Gerais, Brasil	2001	Revista Brasileira de Zoologia
5	Maia	The gall mids (Diptera, Cecidomyiidae) from three restingas of Rio de Janeiro state, Brazil	2001	Revista Brasileira de Zoologia
6	Julião et al.	Galhas de insetos e suas plantas hospedeiras no Pantanal Sul-Mato-Grossense	2002	Naturalia
7	Urso-Guimarães et al.	Occurrence and characterization of entomogen galls in plants from natural vegetation areas in Delfinópolis, MG, Brazil	2003	Brazilian Journal of Biology
8	Maia & Fernandes	Insect galls from Serra de São José (Tiradentes, MG, Brazil)	2004	Brazilian Journal of Biology
9	Oliveira & Maia	Ocorrência e caracterização de galhas de insetos na restinga de Grumani (Rio de Janeiro, RJ, Brasil)	2005	Arquivo do Museu Nacional
10	Urso-Guimarães & Scarelli-Santos	Galls and gall makers in plants from the Pé-de-Gigante Reserve, Santa Rita do Passa Quatro, SP, Brazil	2006	Brazilian Journal of Biology
11	Fernandes & Negreiros	A comunidade de insetos galhadores da RPPN Fazenda Bulcão, Aimorés, Minas Gerais, Brasil	2006	Lundiana
12	Araújo et al.	Galhas entomógenas associadas a vegetação do Parque Estadual da Serra dos Pirineus, Pirenópolis, Goiás, Brasil	2007a	Revista Brasileira de Biociências
13	Araújo et al.	Ocorrência de galhas entomógenas na vegetação do campus da UFG, em Goiânia, Goiás	2007b	Revista Brasileira de Biociências

Table I. (continuation)

N	Author	Title	Year	Journal
14	Maia et al.	Ocorrência e caracterização de galhas de insetos em áreas de Restinga de Bertioga (São Paulo, Brasil)	2008	Biota Neotropica
15	Penteado-Dias & Carvalho	New species of Hymenoptera associated with galls on *Calliandra brevipes* Benth. (Fabaceae, Mimosoideae) in Brazil	2008	Revista Brasileira de Entomologia
16	Carneiro et al.	Insetos indutores de galhas na porção sul da Cadeia do Espinhaço, Minas Gerais, Brasil	2009	Revista Brasileira de Entomologia
17	Carvalho-Fernandes et al.	Galhas entomógenas em um fragmento urbano de Mata Atlântica no centro de endemismo de Pernambuco	2009	Revista Brasileira de Biociências
18	Coelho et al.	Gall inducing arthropods from a seasonally dry tropical Forest in Serra do Cipó, Brazil	2009	Revista Brasileira de Entomologia
19	Maia & Azevedo	Micro-himenópteros associados com galhas de Cecidomyiidae (Diptera) em Restingas do Estado do Rio de Janeiro	2009	Revista Brasileira de Entomologia
20	Bregonci et al.	Insect galls of the Parque Estadual Paulo César Vinha (Guarapiri, ES, Brazil)	2010	Biota Neotropica
21	Maia & Oliveira	Galhas de insetos da Reserva Biológica Estadual da Praia do Sul (Ilha Grande, Angra dos Reis, RJ)	2010	Biota Neotropica
22	Maia et al.	Two new species of *Lopesia* Rubsaamen (Diptera, Cecidomyiidae) associated with *Mimosa hostilis* (Mimosaceae) in Brazil	2010	Revista Brasileira de Entomologia
23	Santos et al.	Ocorrência e caracterização de galhas entomógenas em uma área de floresta estacional semidecídua em Goiânia, Goiás, Brasil	2010	Acta Botanica Brasilica
24	Almada & Fernandes	Insetos indutores de galhas em florestas de terra firme e reflorestamentos com espécies nativas na Amazônia Oriental, Pará, Brasil	2011	Boletim do Museu Paraense Emilio Goeldi de Ciências Naturais
25	Araújo et al.	Insect galls from Serra dos Pirineus, GO, Brazil	2011	Biota Neotropica
26	Maia	Characterization of insect galls, gall makers, and associated fauna of Patô Bacaba (Porto de Trombetas, Pará, Brazil)	2011	Biota Neotropica
27	Santos et al.	Richness of gall-inducing insects in the tropical dry forest (caatinga) of Pernambuco	2011	Revista Brasileira de Entomologia
28	Araújo et al.	Plantas hospedeiras e galhas entomógenas em sub-bosques de florestas tropicais do Pará, Brasil	2012	Insula Revista de Botânica
29	Carvalho-Fernandes et al.	Riqueza de galhas entomógenas em áreas antropizadas e preservadas de caatinga	2012	Revista Árvore
30	Luz et al.	Galhas de insetos em habitas xérico e mésico em região de transição Cerrado Caatinga no norte de Minas Gerais, Brasil	2012	Neotropical Biology and Conservation
31	Malves & Frieiro-Costa	List of plants with galls induced by from the UNILAVRAS/Boqueirão Biological Rserve, Ingaí, state of Minas Gerais, Brazil	2012	Check List
32	Santos et al.	Galhas de insetos em área de cerrado sentido restrito na região semi-urbana de Caldas Novas (Goiás, Brasil)	2012	Revista Brasileira de Entomologia

Table I. (continuation)

N	Author	Title	Year	Journal
33	Coelho et al.	Gall-inducing from Serra do Cabral, Minas Gerais, Brazil	2013	Biota Neotropica
34	Maia	Insect galls of São Tomé das Letras (MG, Brazil)	2013	Biota Neotropica
35	Costa et al.	Galhas entomógenas associadas à Leguminosae do entorno do riacho Jatobá, Caetité, Bahia, Brasil	2014a	Revista Brasileira de Biociências
36	Costa et al.	Galhas de insetos em uma área de transição caatinga-cerrado no Nordeste do Brasil	2014b	Sitientibus série Ciências Biológicas
37	Maia	Insect galls of Itamonte (Minas Gerais, Brazil): characterization and occurrence	2014	Biota Neotropica
38	Maia et al.	Insect galls from Atlantic Forest areas of Santa Teresa, Espírito Santo, Brazil: characterization and occurrence	2014	Boletim do Museu de Biologia Mello Leitão
39	Carvalho et al.	Ocorrência de galhas entomógenas em plantas do Parque Florestal dos Pioneiros, em Maringá, Paraná, Brasil	2015	Revista Uningá Review
40	Santos & Ribeiro	Ocorrência e caracterização de galhas em fragmento de floresta estacional semidecidual em Telêmanco Borba, Paraná, Brasil	2015	Revista Semina: Ciências Biológicas e da Saúde
41	Suzuki et al.	Detection and distribution of cell growth regulators and cellulose microfibrils during the development of *Lopesia* sp. galls on *Lonchocarpus cultratus* (Fabaceae)	2015	Botany
42	Carvalho-Fernandes et al.	Diversity of insect galls associated with coastal shrub vegetation in Rio de Janeiro, Brazil	2016	Anais da Academia Brasileira de Ciências
43	Maia & Carvalho-Fernandes	Insect galls of a protected remnant of Atlantic Forest tableland from Rio de Janeiro State (Brazil)	2016	Revista Brasileira de Entomologia
44	Maia & Silva	Insect galls of Restinga de Marambaia (Barra de Guaratiba, Rio de Janeiro, RJ)	2016	Brazilian Journal of Biology
45	Nogueira et al.	Insect galls from Serra Geral, Caetité, BA, Brazil	2016	Biota Neotropica
46	Alcântara et al.	Ocorrência e caracterização de galhas em duas áreas do noroeste do Ceará, Brasil	2017	Natureza on line
47	Bergamini et al.	Occurrence and characterization of insect galls in the Floresta Nacional de Silvania, Brazil	2017	Papéis avulsos de Zoologia
48	Maia & Mascarenhas	Insect galls of the Parque Nacional do Itatiaia (Southeast Region, Brazil)	2017	Anais da Academia Brasileira de Ciências
49	Urso-Guimarães et al.	Characterization of entomogen galls from Mato Grosso do Sul, Brazil	2017	Revista Brasileira de Entomologia
50	Ascendino & Maia	Insects galls of Pantanal areas in the State of Mato Grosso do Sul, Brazil: characterization and occurrence	2018	Anais da Academia Brasileira de Ciências
51	Brito et al.	Riqueza de galhas de insetos em áreas de caatinga com diferentes graus de antropização do estado da Bahia, Brasil	2018	Iheringia, Série Zoologia

Table I. (continuation)

N	Author	Title	Year	Journal
52	Costa et al.	Biology and development of galls induced by *Lopesia* sp. (Diptera: Cecidomyiidae) on leaves of *Mimosa gemmulata* (Leguminosae: Caesalpinioideae)	2018	Australian Journal of Botany
53	Flor et al.	Insect galls of the Floresta da Cicuta (Volta Redonda, RJ, Brazil)	2018	Papéis Avulsos de Zoologia
54	Lima & Calado	Morphological characterization of insect galls and new records of associated invertebrates in a Cerrado area in Bahia State, Brazil	2018	Brazilian Journal of Biology
55	Nogueira et al.	Structural and histochemical profile of *Lopesia* sp. Rübsaamen 1908 pinnula galls on *Mimosa tenuiflora* (Willd.) Poir. in a Caatinga environment	2018	Hoehnea
56	Santos et al.	Insect galls in three species of *Copaifera* L. (Leguminosae, Caesalpinioideae) occurring sympatrically in a Cerrado area (Bahia, Brazil)	2018	Biota Neotropica
57	Silva et al.	Insect gall occurrence in savanna and forest remnant sites of Hidrolândia, GO, Brazil Central	2018	Papéis Avulsos de Zoologia
58	Vieira et al.	Insect galls in Rupestrian field and Cerrado *stricto sensu* vegetation in Caetité, Bahia, Brazil	2018	Biota Neotropica

Table II. The first records of gall-inducing insects associated with Fabaceae undertaken by the naturalist J.S. Tavares between 1905 and 1925 (Gagné & Jaschhof 2017).

Inducer	Plant host	Occurrence
Anadiplosis caetetensis Tavares, 1920e	Fabaceae Indet.	Bahia, Caetité
Anadiplosis procera Tavares, 1920e	Mimosoideae Indet. (=Caesalpinioideae)	Bahia, Salvador
Anadiplosis pulchra Tavares, 1916a	*Machaerium* sp.	Rio de Janeiro, Nova Friburgo
Anadiplosis venusta Tavares, 1916a	*Machaerium* sp.	Rio de Janeiro, Nova Friburgo
Andirodiplosis bahiensis Tavares, 1920d	*Andira* sp.	Bahia, Salvador
Eudiplosis parva Tavares, 1916a	Fabaceae Indet.	Bahia, Salvador
Schizomyia mimosae Tavares, 1925a	*Mimosa caesalpiniifolia* Benth.	Ceará

Table III. Numbers of Fabaceae taxa hosting galls in different Brazilian phytogeographical domain.

Biome	N° of genera	N° of species in Brazil	N° of host species	Numbers of morphotypes
Amazon Forest	164	1,144	44	73
Atlantic Forest	156	1,005	47	89
Caatinga	128	609	22	50
Cerrado	138	1,263	59	196
Pantanal	67	167	14	30

Table IV. Gall morphotypes reported in Fabaceae in Brazil.

Shape	Number
Globoid	142
Lenticular	104
Fusiform	87
Amorphous	43
Cylindrical	21
Conical	20
Marginal roll	10
Parenchymatous	5
Leaf fold	4
Rosette	2

DISCUSSION

A large number of published (58) papers about galls associated with Fabaceae in Brazil have been published on different journals, and it continues to grow. Three Brazilian journals, Biota Neotropica, Revista Brasileira de Entomologia, and Brazilian Journal of Biology, were the most relevant in terms of number of publications. These were the same scientific journals that published the most papers about Brazilian insect galls during the last 30 years (Araújo 2018). Different aspects of insect gall induced on Fabaceae have been studied in Brazil, approximately 86% of the publications described the insect gall diversity and their plant hosts at different sites. Other studies that recorded observations of galls on Brazilian Fabaceae had as their focused included papers on plant anatomy, ecology, and taxonomy; these papers represented 13.7% of the papers surveyed (Table I).

The Fabaceae host a wide variety of gall morphotypes in different Brazilian phytogeographical domains, including the Caatinga (Carvalho-Fernandes et al. 2012, Alcântara et al. 2017, Brito et al. 2018), Atlantic forest (Fernandes & Negreiros 2006, Maia & Oliveira 2010, Maia & Silva 2016), Pantanal (Julião et al. 2002), and Amazon forest (Maia 2011, Almada & Fernandes 2011), with the highest number of plant host species (n=59) and distinct gall morphotypes (n=196) being found in Cerrado (Table IV). That gall richness reflects the

Figure 1. Insect galls associated on Fabaceae occurring in Brazil. 1-4, *Bauhinia pulchella* Benth., 5-6, *Bauhinia* sp., 7-8, *Bauhinia acuruana* Moric., 9-10, *Calliandra macrocalyx* Hamrs, 11-12, *Copaifera langsdorffii* Desf. Images: Tainar Araujo.

high number of Fabaceae species encountered in the Cerrado phytogeographical domain (ca. 1,263) (BFG 2015). However, these numbers for relative diversity of gall morphotypes and host plant species could be an artifact of sampling due to the known diversity of galls in Brazil is largely based on studies undertaken in Cerrado phytogeographical domain.

The great majority of host plants were identified to species (n=178); this is a reflection of the relatively large number of taxonomists studying legumes in Brazil, and many of the voucher specimens are of good quality.

Among the six subfamilies currently recognized for the Fabaceae, five host gall-inducing insects in Brazil – Caesalpinioideae, Cercidoideae, Detarioideae, Dialioideae, and Papilionoideae. Duparquetioideae, the only subfamily not recorded hosting galls in that country, is monospecific, and its single species (*Duparquetia orchidacea* Baill.) is native to tropical Africa (Lewis et al. 2005).

The genus showing the greatest gall richness was *Inga*. That taxon comprises a large number of species (ca. 300) widely distributed in the neotropical region, with representatives present from one end of the humid tropical zone to the other (from Mexico to Uruguay), as well as in the Greater and Lesser Antilles (Pennington 1997). Brazil is estimated to have 132 species of *Inga*, of which 51 are endemic (BFG 2015). A significant number of species of that genus are widely distributed – favoring their association with gall-inducing insects.

Copaifera langsdorffii stands out among super-host Fabaceae species in Brazil, especially in Cerrado vegetation (Fernandes et al. 1998, Costa et al. 2010, Luz et al. 2012). Twenty eight gall morphotypes have been recorded on that species (*e.g.*, Gonçalves-Alvim & Fernandes 2001, Maia & Fernandes 2004, Costa et al. 2010, Luz et al. 2012, Santos et al. 2012), and it is considered one of the principal super-hosts of galls throughout the neotropical region (Oliveira & Isaias 2009).

Galls can be induced on the leaves, stems, buds, branches, flower buds, flowers, and fruits of host plants (Figure 2). Most galls have been observed on leaves (n=306), corroborating the global pattern described by Mani (1964). According to that author, leaves have greater abundances of nutrients and mineral resources than other plant organs, favoring the greater incidence of galls. The second most prevalent plant organ where galls occur is the stem (n=102). Galls were likewise encountered on leaf

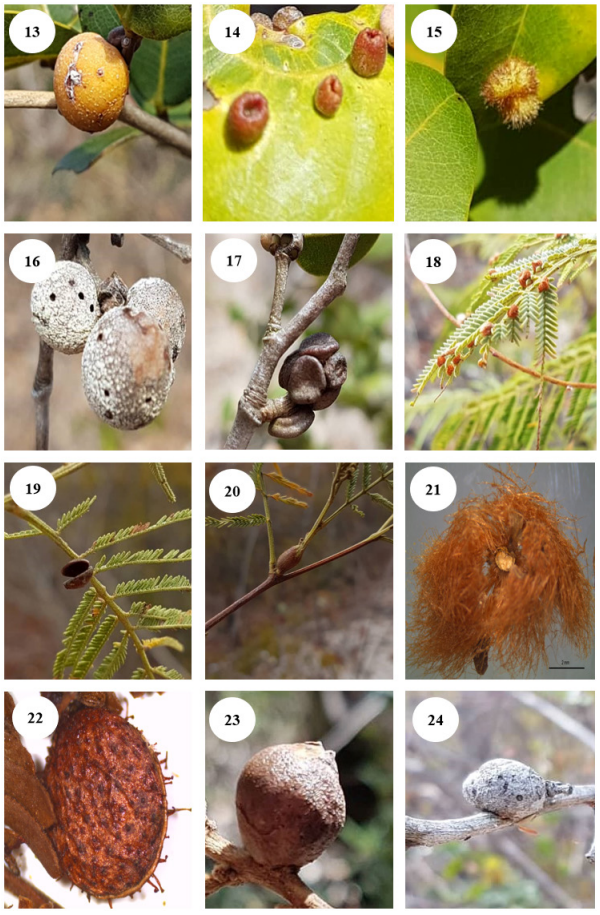

Figure 2. Insect galls associated on Fabaceae occurring in Brazil. 13-14, *Copaifera langsdorffii* Desf., 15-17, *Copaifera sabulicola* J.A.S. Costa & L.P. Queiroz., 18-21, *Mimosa gemmulata* Barneby, 22, *Mimosa tenuiflora* (Willd.) Poir., 23, *Senegalia* sp., 24, *Senegalia langsdorffi* (Benth.) Seigler & Ebinger. Images: Tainar Araújo (13-20; 23-24) and Juliana Santos (21-22).

buds, branches, shoots, inflorescences, flower buds and fruits, although at lower frequencies. A predominance of galls on leaves and stems has also been observed in other plant families, such as Asteraceae, Melastomataceae, and Myrtaceae (Malves & Frieiro-Costa 2012, Maia 2013, 2014, Maia & Carvalho-Fernandes 2016).

Most gall morphotypes occur on a single plant organ, but there are records of galls forming on both the leaves and buds of *Machaerium nyctitans* (Vell.) Benth. (Papilionoideae) and *Mimosa melanocarpa* Benth. (Caesalpinioideae) (Maia & Mascarenhas 2017).

The galls induced on Fabaceae demonstrate a wide variety of shapes, varying from simple intumescences to complex structures resembling fruits. Nine distinct gall shapes were recorded, with globoid shape being most common (32% of the morphotypes reported) (Table IV). Globoid galls have been the predominant morphotype in all of the inventories undertaken in the neotropical region (Isaias et al. 2013).

The insect inducers of gall morphotypes were examined in Brazil; 145 of the 293 were identified to order or family. Representatives of the orders Coleoptera, Diptera, Hymenoptera, Hemiptera, Lepidoptera, and Thysanoptera have been identified as gall-inducing insects, with Cecidomyiidae (Diptera) inducing the most gall morphotypes (n= 252) – similar to the general pattern recorded for the neotropics. Six insect orders have gall-inducing representatives in the neotropics: Diptera, Lepidoptera, Hymenoptera, Coleoptera, Hemiptera, and Thysanoptera. Diptera predominate among them, with more than 1,000 gall morphotypes reported, induced principally by Cecidomyiidae (Maia et al. 2008).

Cecidomyiidae stands out as the principal insect family inducing galls in many Fabaceae species, for example on *Andira paniculata* Benth. (=*Andira vermifuga* [Mart.] Benth.) (Santos et al. 2012), *Bauhinia brevipes*, *Calliandra dysantha* Benth., *Copaifera langsdorffii*, *Hymenaea courbaril* L., *Platymiscium floribundum* Vogel (Luz et al. 2012), *Bauhinia acuruana* Moric. (Nogueira et al. 2016), *Mimosa tenuiflora* (Brito et al. 2018), and *Mimosa gemmulata* Barneby (Vieira et al. 2018). Some new species of Cecidomyiidae are responsible for inducing galls in Fabaceae were recently described from Brazil, for example, *Lopesia grandis* Maia, 2001 on *Dalbergia ecastaphyllum* (L.) Taub.; *Lopesia aldinae* Fernandes & Maia, 2010 on *Aldina heterophylla* Spruce ex Benth.; *Lopesia mimosae* Maia, 2010 and *Lopesia pernambucensis* Maia,

2010 on *Mimosa hostilis* Benth. (=*Mimosa tenuiflora*); *Lopesia chapadensis* Garcia & Urso-Guimarães, 2018 on *Andira vermifuga* (Mart.) Benth. (Maia 2001, Fernandes et al. 2010, Maia et al. 2010, Garcia & Urso-Guimarães 2018).

Sixty-three gall morphotypes observed on Brazilian Fabaceae were found to be inhabited by representatives of the orders Coleoptera, Collembola, Diptera, Formicidae, Hemiptera, Hymenoptera, Lepidoptera, Pseudoscorpionida, and Thysanoptera – composing an associated fauna (Table SI). Those inhabitants can be classified according to their lifestyles as inquilines, predators, or parasitoids that inhabit galls still occupied by the inducer insect, or as successors in galls abandoned by their inducers (and generally decomposing) (Maia et al. 2008).

Parasitoids belonging to the order Hymenoptera in Fabaceae galls are relatively common and diverse, observed to be associated with 74 gall morphotypes. Micro-hymenoptera are the principal parasites of gall-inducing insects, and can be responsible for their mortality (Maia et al. 2008). According to Stone et al. (2002), approximately 115,000 species of Hymenoptera are found throughout the world, and they have been recorded in the galls of various species of Fabaceae (*e.g.*, *Andira paniculata* Benth., *Copaifera sabulicola, Copaifera luetzelburgii* Harms, *Copaifera depilis* Dwyer) (Santos et al. 2018).

The Fabaceae are the principal super-hosts of galls in Brazil; they also comprise one of the most highly diverse families of angiosperms in that country, together with Orchidaceae, Asteraceae, Rubiaceae, Melastomataceae, Bromeliaceae, Poaceae, Myrtaceae, Euphorbiaceae, Malvaceae, and Malpighiaceae (Table V). Our results confirm that galling species will increase as the number of recorded host plant species increases and with plant families or genera size, aggregating evidences for the hypotheses of plant species richness (Fernandes & Price 1988, Wright & Samways 1998, Cuevas-Reyes et al. 2004, Mendonça Júnior 2007) and of taxon size (Cornell 1985, Gonçalves-Alvim & Fernandes 2001, Veldtman & Mcgeoch 2003, Mendonça Júnior 2007). In spite of the already large number of insect inductors of galls known to be associated with the Fabaceae, that total could easily increase with more intensive studies.

Table V. Richness of galls associated with the principal angiosperm families in Brazil.

Family	N° of species in Brazil	N° of host species	Numbers of morphotypes
Asteraceae	2,097	122	316
Bromeliaceae	1,340	0	0
Euphorbiaceae	946	44	90
Leguminosae	2,848	178	438
Malpighiaceae	572	42	110
Malvaceae	785	11	16
Melastomataceae	1,419	66	138
Myrtaceae	1,030	57	169
Orchidaceae	2,475	1	1
Poaceae	1,483	1	1
Rubiaceae	1,415	36	69

The co-evolution of Fabaceae species and gall-inducing insects has given rise to a wide variety of associations that still require in-depth biological and ecological examination, for relatively little is currently known about their ontogeny, structure, chemistry (*e.g.*, Isaias 1998, Isaias et al. 2006, Oliveira & Isaias 2009, 2010, Sá et al. 2009, Suzuki et al. 2015, Costa et al. 2018, Nogueira et al. 2018) or ecology (Almeida et al. 2006). The synthesis provided in the current

study concerning the established interactions between gall-inducing insects and the Fabaceae can provide the basis for new studies and new perspectives on their evolutionary ecology.

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SUPPLEMENTARY MATERIAL

Table SI.

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