



An overview of inventories of gall-inducing insects in Brazil: looking for patterns and identifying knowledge gaps

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Abstract: We compiled published Brazilian gall-inducing insect inventories aiming to understand trends and biases in this field research and to investigate the factors that potentially explain the diversity of gall-inducing insects among different sampling sites. A total of 51 studies with gall-inducing insect inventories were compiled for Brazil, which sampled 151 sites in 88 municipalities, 13 states and five regions. The number of papers published on gall-inducing insects per year has increased over the last 30 years, being Cecidomyiidae (Diptera) the main galling taxon, Fabaceae the main host-plant family and *Protium heptaphyllum* (Burseraceae) the most important super-host species in these inventories. We found a great bias in the geographical distribution of Brazilian inventories, with the majority of studies in the Southeast region, and Atlantic Forest and Cerrado biomes. The total richness of gall-inducing insects differed significantly among regions and biomes, with higher gall richesses being recorded in the North region and Amazon biome. However, Brazilian regions and biomes did not vary in richness of gall-inducing insect morphotypes per plant species. According our results, sampling by cecidologists in less studied regions of Brazil is needed, particularly in the North and South regions and subsampled biomes such as the Amazon, Pampas and Pantanal.

Key words: Atlantic Forest, Cecidomyiidae, Cerrado, Fabaceae, gall-inducing insects.

INTRODUCTION

Brazil is a mega-diverse country in terms of biodiversity (Lewinsohn and Prado 2005). Estimates suggest that Brazil possesses the richest flora of the world with about 40,000 species, almost 19,000

(46%) of which are endemic (Forzza et al. 2012).

This high number of plant species represents a great diversity of potential niches for gall-inducing insects (Fernandes 1992, Mendonça 2007). Galling insects are very specialized herbivores known to be highly specific to their host plants (Mani 2013, Stone and Schönrogge 2003). Estimates of the global richness of gall-inducing insects point to approximately 133,000 species, with most of them

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occurring in the Neotropical region (Espírito-Santo and Fernandes 2007). The great richness of flora and number of gall-inducing insects that they can potentially host has resulted in a large number of studies inventorying insect gall diversity in Brazil in recent decades.

Inventories of gall-inducing insects have been performed in Brazil since the 1980's. For example, in a pioneering study Fernandes et al. (1988) investigated the occurrence of gall-inducing insects in Cerrado vegetation of the Pampulha Campus in Minas Gerais State, recording 37 insect galling species on 22 host plant species. More recently, Urso-Guimarães et al. (2017) performed inventories in four biomes in Mato Grosso do Sul State (Atlantic Forest, Cerrado, Chaco and Pantanal), recording a total of 186 insect galling species on 115 host plant species. These studies illustrate that during the last few decades many inventories have been published for several regions and biomes of Brazil. Inventories of gall-inducing insects performed in Brazil represent a good proportion of the scientific production about insect galls in Latin America (Grandez-Rios et al. 2015).

Interest about gall-inducing insects has promoted great contributions to the ecological and evolutionary understanding of insect-plant interactions (Araújo et al. 2014a), and also in applied areas such as agriculture, biological control and nature conservation (Grandez-Rios et al. 2015). Studies in galling insect ecology have clarified community structure throughout three trophic levels: host plants, herbivores as well as their natural enemies (Mendonça 2007, Araújo et al. 2014a). Research advances have also provided basic information for applied ecology, for example, in the agriculture and biological control due many gall-inducing insects attacks cultivated plants (Grandez-Rios et al. 2015) and in the conservation of natural areas, because galling insects can be used as biological indicators of habitat quality (Moreira et al. 2007, Araújo et al. 2014a).

Despite the growing number of gall-inducing insect inventories in Brazil, there is no compilation of the main trends and patterns of this research. Therefore, the aim of the present study was to understand the trends and biases among Brazilian galling insect inventories to better evaluate whether efforts have been well applied and to identify future challenges for Brazilian cecidologists. Thus, this study seeks to answer the following questions: (1) How are inventories distributed among Brazilian geographic regions and biomes? (2) Is there a temporal trend in the number of studies published on the topic? (3) Which taxa of host plants and galling insects are most frequently recorded among Brazilian inventories? (4) Do latitude and elevation affect the diversity of gall-inducing insects? and (5) Does gall-inducing insect diversity vary among Brazilian regions, biomes, and vegetation types?

MATERIALS AND METHODS

Gall-inducing insect inventories performed in Brazil were compiled from papers published between 1988 and 2017. Papers were considered inventories only if they possessed data collected in the field that included sampling of the community of host plants. Inventories were included in the compilation only when it was explicitly indicated that the study was fully or partially performed within the territory of Brazil. To give an overview of trends with Brazilian gall-inducing insect inventories, papers were classified by location (Brazilian region, state and city), habitat (biome and vegetation type), host plant taxa (super-host families and species) and gall-inducing insect taxa (proportion of gall-inducing insects induced by Cecidomyiidae), according to the content and descriptions provided by the cecidologists or taxonomists. Inventories carried out in more than two locations or habitats were included under each involved. All compiled inventories were performed

in natural vegetation, but the vegetation sampled varied in the state of conservation.

The total richness of gall-inducing insects and the richness of gall morphotypes per plant species were used as variables of insect gall diversity. These variables were analyzed per sampling site (and not per paper) because many inventories were performed in several sample sites simultaneously (e.g., Fernandes et al. 2001, Santos et al. 2011a, Urso-Guimarães et al. 2017). Sampling sites were considered as different when it was explicitly indicated by the authors that sampling was done in distinct and discontinuous areas and/or distinct phytogeographies (from the availability of geographic coordinates), and also when the gall-inducing insects and the host plants were presented separately for each site. When it was indicated that different points were sampled within the same sampling area (e.g., conservation unit), and/or geographical coordinates that allowed the spatial differentiation of points were not provided, sampling was considered, for the purposes of this study, to have been performed at only one sampling site.

The temporal trend in the number of publications including gall-inducing insect inventories per year in Brazil was evaluated using Pearson correlation. Spearman rank correlations were used to relate gall-inducing insect variables (total richness of gall-inducing insects and the richness of gall morphotypes per plant species) with latitude and elevation of each sampling site. These variables were obtained from descriptions provided by the authors or, when absent, from the coordinates of the municipality where the sampling site was located. Coordinates were converted to decimal degrees using the online converter available at <https://www.latlong.net/>. Additionally, gall-inducing insect variables were contrasted among regions, biomes, and vegetation types using Kruskal-Wallis tests. For a better visualization of the results, data are presented in the text as mean \pm SD (standard deviation).

RESULTS

A total of 51 studies on gall-inducing insect inventories were compiled for Brazil (Table I), which sampled 151 sites in 88 municipalities, 13 states and five regions (Figure 1). The number of papers published on gall-inducing insects per year has increased over the last 30 years ($R_{Pearson} = 0.628$; $N = 19$; $P < 0.01$; Figure 2). Most Brazilian inventories were for the Southeast (58.8%), Midwest (15.6%) and Northeast (15.6%) regions, and for Minas Gerais (33.3%) and Rio de Janeiro (19.6%) states. The Atlantic Forest and Cerrado were the most studied Brazilian biomes, with 23 and 22 studies, respectively.

The number of insect gall morphotypes ranged from 22 to 432 species (109.6 ± 75.7), and the number of host plants from 14 to 255 species (63.3 ± 47.7). The mean number of insect gall morphotypes per plant species was $1.72 (\pm 0.43)$, ranging between 1.16 and 3.50. The richness of gall-inducing Cecidomyiidae (Diptera) ranged from 5 to 301, and represented between 14.3% and 97.8% of the gall-inducing insects cited in the Brazilian insect gall inventories (Table I). Fabaceae was the most important plant family in the Brazilian inventories, appearing as a super-host in 68.6% of the studies, and as having the greatest gall-inducing insect richness in 22 studies (Table I). Myrtaceae and Asteraceae were also important host families, being super-hosts in 49.0% and 37.2% of the studies, and most diverse in eight studies each. The most frequent species listed as super-host plants were *Protium heptaphyllum* (Burseraceae) and *Copaifera langsdorffii* (Fabaceae), which were recorded in seven (13.7%) and six (11.7%) studies, respectively.

The total richness of gall-inducing insects and the richness of insect gall morphotypes per plant species were not influenced by latitude or elevation (all $R_{Spearman}$ values < 0.20 and P values > 0.05 ; Figure 3). On the other hand, the total richness of gall-inducing insects differed significantly among

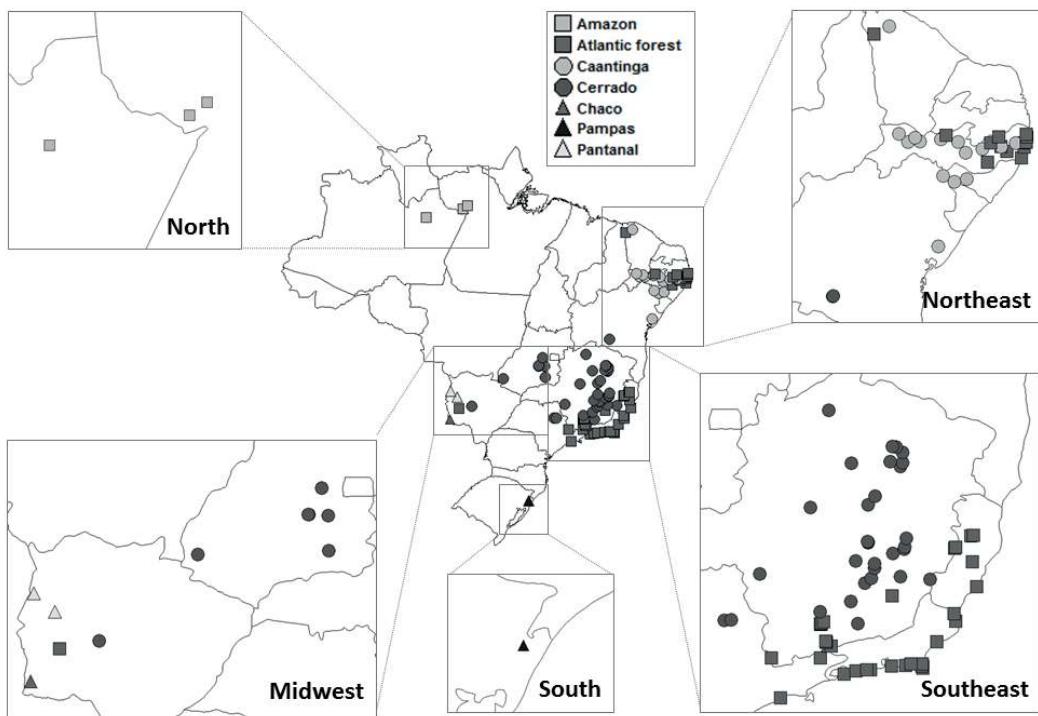


Figure 1 - Distribution of sites where gall-inducing insects were sampled in different biomes and regions in Brazil. At this map scale some of sites are located so close to another that they are indistinguishable.

regions ($H = 13.807$; $N = 74$; $P < 0.01$), and biomes ($H = 8.333$; $N = 87$; $P < 0.02$). The highest gall richnesses were recorded in the North region (Figure 4a) and Amazon biome (Figure 4b), both with $181.2 (\pm 107.0)$ gall morphotypes. However, Brazilian regions and biomes did not vary in the richness of gall-inducing insect morphotypes per plant species (P values > 0.05 ; Figure 4c and 4d, respectively). Similarly, the gall-inducing insect variables did not differ among vegetation types ($P > 0.05$).

DISCUSSION

The results obtained from the compilation of Brazilian gall-inducing insect inventories reveal important trends and biases. First, there was a significant positive trend in the number of papers published in the country, especially over the last decade. This result is likely a direct consequence of

the intensive effort of several researchers to gather data on the biodiversity of insect galls, mainly as a result of the establishment of the Brazilian Symposium on Galls and Gallers (in Portuguese: Simpósio Brasileiro sobre Galhas e Galhadores), which has been held biannually at the Brazilian Congress of Zoology (since 2012). These efforts have resulted in a broadening of gall-inducing insect sampling in different Brazilian regions, with almost all of the studies carried out in the Southeast region of Brazil being published in the last 10 years (see Table I). This large and growing number of insect gall inventories confirms the Brazil as the most important research center about gall-inducing insects in Latin America and one of the most important in the world. This result is in agreement with Grandez-Rios et al. (2015), which argue that Brazil is responsible for about 70% of Latin American scientific production on gall-inducing insects.

TABLE I
Inventories of gall-inducing insects realized in Brazil between 1988 and 2017.

Inventories	Brazilian regions	Brazilian states	Biomes	Gall-inducing insect richness	Plant species richness	Plant family richness	Plant morphotypes per plant species	Number of gall morphotypes	Super-host families (number of insect gall morphotypes)	Super-host species (number of insect gall morphotypes)	Richness of Cecidomyiidae	% of Cecidomyiidae
Alcântara et al. 2017	Northeast	CE	Caatinga-Atlantic forest	48	19	17	2.53	(8)	Euphorbiaceae (3)	<i>heptaphyllum</i> (16), <i>Croton sonderianus</i> (8)	NI	NI
Almada et al. 2011	North	PA	Amazon	309	255	45	1.21	(12)	Fabaceae (87), Chrysobalanaceae (6), Burseraceae (5), <i>Protium heptaphyllum</i> (16), <i>Tapirira guianensis</i> (6), <i>Vismia latifolia</i> (5), <i>Endoplectura uchi</i> (4)	301	97.4	
Araújo et al. 2011	Midwest	GO	Cerrado	62	51	28	1.22	(18)	Fabaceae (8), Styracaceae (6), Malpighiaceae (5)	<i>Andira paniculata</i> (3), <i>Qualea parviflora</i> (3)	22	35.5
Araújo et al. 2012	North	PA	Amazon	112	65	33	1.72	(14)	Fabaceae (18), Bignoniaceae (14), Lauraceae (12)	<i>Adenocalymma neoflavidum</i> (9), <i>Ocotea</i> sp. (6), <i>Inga</i> <td>NI</td> <td>NI</td>	NI	NI
Araújo et al. 2014c	Midwest	GO	Cerrado	97	55	24	1.76	(12)	Myrtaceae (17), Fabaceae (14), Vochysiaceae (9)	<i>Andira cuyabensis</i> (4), <i>Myrcia guianensis</i> (4)	37	38.1
Bergamini et al. 2017	Midwest	GO	Cerrado	186	61	35	3.05	(12)	Fabaceae (18), Asteraceae (17), Sapindaceae (16)	<i>heptaphyllum</i> (14), <i>Siparuna guianensis</i> (12), <i>Serjania</i> sp. (12)	64	34.4

TABLE I (continuation)

Inventories	Brazilian regions	Brazilian states	Biomes	Gall-inducing insect richness	Plant species richness	Plant family richness	Plant per plant richness	Number of gall morphotypes	Super-host families (number of insect gall morphotypes)	Richness of insect (number of gall morphotypes)	% of Cecidomyiidae	Cecidomyiidae
Bregonci et al. 2010	Southeast	ES	Atlantic Forest	38	21	17	1.81	(7)	Myrtaceae (4), <i>Myrciaria floribunda</i> (4)	Andira nitida (3), <i>Manilkara subsericea</i> (3)	84.2	32
Carneiro et al. 2009	Southeast	MG	Cerrado	241	142	29	1.70	(4)	Asteraceae (86), Melastomataceae (22), Malpighiaceae (18)	<i>pseudomyriocphala</i> (3), <i>Baccharis pseudomyriocphala</i> (10), <i>Byrsinima coccobifolia</i> (8), <i>Baccharis planypoda</i> (7)	85.1	205
Carvalho-Fernandes et al. 2012	Northeast	AL, BA, SE	Caatinga	25	18	8	1.39	(4)	Fabaceae (11), Euphorbiaceae (4), Boraginaceae (3)	<i>Caesalpinia pyramidalis</i> (4), <i>Eugenia copacabensis</i> (9)	40.0	10
Carvalho-Fernandes et al. 2016	Southeast	RJ	Atlantic Forest	151	82	34	1.84	(3)	Rubiaceae (9)	<i>Baccharis dracunculifolia</i> (22), <i>Eugenia copacabensis</i> (9)	62.9	95
Coelho et al. 2009	Southeast	MG	Cerrado	92	51	17	1.80	(1)	Fabaceae (14), Rubiaceae (8)	<i>Myrtaceae</i> (11), <i>Asteraceae</i> (8), <i>Baccharis brasiliensis</i> (5)	76.1	70
Coelho et al. 2013a	Southeast	ES, MG, RJ	Cerrado, Atlantic Forest	93	50	13	1.86	(17)	Myrtaceae (52), Melastomataceae (8), <i>trichotoma</i> (5), <i>Celtis brasiliensis</i> (5)	<i>Baccharis planypoda</i> (8), <i>Baccharis trichotoma</i> (5), <i>Celtis brasiliensis</i> (5)	97.8	91
Coelho et al. 2013b	Southeast	MG	Cerrado	47	39	21	1.21	(9)	Asteraceae (12), Malpighiaceae (4)	<i>Byrsinima salzmannii</i> (6), <i>guilleminiana</i> (3)	44	44

TABLE I (continuation)

Inventories	Brazilian regions	Brazilian states	Biomes	Gall-inducing insect richness	Plant species richness	Plant family richness	Plant richness per plant species	Number of gall morphotypes	families (number of insect gall morphotypes)	Super-host families (number of insect gall morphotypes)	Richness of Cecidomyiidae	% of Cecidomyiidae
Costa et al. 2014	Northeast	BA	Caatinga-Cerrado	43	33	17	1.30	Fabaceae (15), Myrtaceae (5)	Bauhinia pulchella (3)	Bauhinia pulchella (15)	15	34.9
Fernandes and Negrerios 2006	Southeast	MG	Atlantic Forest	30	25	12	1.20	Euphorbiaceae (6), Euphorbiaceae (4)	Cordia sellowiana (3)	Cordia sellowiana (28)	28	93.3
Fernandes et al. 1988	Southeast	MG	Cerrado	37	22	11	1.68	Fabaceae (15), Boraginaceae (5)	Copafera langsdorffii (7), Fabaceae (34), Malpighiaceae (32), Asteraceae (32)	Copafera langsdorffii (21)	21	56.8
Fernandes et al. 1997	Southeast	MG	Cerrado	236	134	27	1.76	Boraginaceae (5)	Cordia sellowiana (4), Sida urens (6)	Cordia sellowiana (195)	195	82.6
Fernandes et al. 2001	Southeast	MG	Atlantic Forest	273	139	40	1.96	Asteraceae (17), Myrsinaceae (16), Bignoniaceae (16)	Myrcia multiflora (9), Vernonia polyanthes (9), Eremanthus sp. (8)	Myrcia multiflora (225)	225	82.4
Fernandes et al. 2009	Northeast	PE	Atlantic Forest	32	16	13	2.00	Lecythidaceae (5)	Protium heptaphyllum (5)	Protium heptaphyllum (5)	5	15.6
Gonçalves- Alvim and Fernandes 2001	Southeast	MG	Cerrado	92	62	28	1.48	Burseraceae (5), Asteraceae (5), Malpighiaceae (5)	Byrsinima coccobifolia (4), Andira sp. (4), Myrcia sp. (4)	Byrsinima coccobifolia (69)	69	75.0

TABLE I (continuation)

Inventories	Brazilian regions	Brazilian states	Biomes	Gall-inducing insect richness	Plant species richness	Plant family richness	Plant per plant richness	Number of gall morphotypes	Number families (number of insect gall morphotypes)	Super-host species (number of insect gall morphotypes)	Richness of Cecidomyiidae	% of Cecidomyiidae
Julião et al. 2002	Midwest	MS	Pantanal	133	75	37	1.77	(10), Fabaceae (6), Sapindaceae	(10), Fabaceae (6), <i>Inga vera</i> (5)	<i>Hippocratea volubis</i> (6), <i>Inga vera</i> (5)	130	97.7
Julião et al. 2017	North	AM	Amazon	228	169	38	1.35	Burseraceae (28), Fabaceae (28), Chrysobalanaceae (5)	Burseraceae (28), Fabaceae (28), Chrysobalanaceae (5)	<i>Protium pilosissimum</i> (5)	NI	NI
Luz et al. 2012	Southeast	MG	Cerrado-Caatinga	98	70	20	1.40	Fabaceae (19), Myrtaceae (6), Sapindaceae (4)	Fabaceae (19), Myrtaceae (6), Sapindaceae (4)	<i>langsdorffii</i> (11), <i>Calophyllum brasiliense</i> (5), <i>Bauhinia brevipes</i> (4)	59	60.2
Maia and Carvalho-Fernandes 2016	Southeast	RJ	Atlantic Forest	143	82	31	1.74	Fabaceae (28), Myrtaceae (13), Sapindaceae (13)	Fabaceae (28), Myrtaceae (13), Sapindaceae (13)	<i>Prostremma heptaphyllum</i> (4)	39	27.3
Maia and Fernandes 2004	Southeast	MG	Cerrado	137	73	30	1.88	Fabaceae (20), Myrtaceae (18), Asteraceae (16)	Fabaceae (20), Myrtaceae (18), Asteraceae (16)	<i>heptaphyllum</i> (7), <i>Coparia</i> <i>langsdorffii</i> (6), <i>Myrcia</i> sp. (6)	101	73.7
Maia and Mascarenhas 2017	Southeast	ES, MG, RJ	Atlantic Forest	432	145	47	2.97	Melastomataceae (66), Fabaceae	Melastomataceae (66), Fabaceae	<i>Mikania glomerata</i> (8), <i>Mikania</i> sp. (8), <i>Myrcia sylvatica</i> (8)	152	64.9
Maia and Oliveira 2010	Southeast	RJ	Atlantic Forest	36	22	16	1.64	Asteraceae (5) e	Myrtaceae (9), <i>Mikania</i> sp. (4), <i>Guapira opposita</i> (4)	NI	27	

TABLE I (continuation)

Inventories	Brazilian regions	Brazilian states	Biomes	Gall-inducing insect richness	Plant species richness	Plant family richness	Plant richness per plant species	Number of gall morphotypes	Number of insect gall morphotypes	Super-host families (number of insect gall morphotypes)	Super-host species (number of insect gall morphotypes)	Richness of Cecidomyiidae	% of Cecidomyiidae
Maia and Silva 2016	Southeast	RJ	Atlantic Forest	31	24	16	1.29	Myrtaceae (6), Fabaceae (4), Malpighiaceae (4)	Myrtaceae (6), <i>Erythroxylum ovalifolium</i> (3), <i>Byrsomima sericea</i> (3)	(3), <i>Erythroxylum ovalifolium</i> (3), <i>Guapira opposita</i> (3), <i>Tournefortia membranacea</i> (3), <i>Eugenia uniflora</i> (3)	25	80.6	
Maia and Souza 2013	Southeast	RJ	Atlantic Forest	45	29	18	1.55	Asteraceae (7), Myrtaceae (6)	Asteraceae (7), <i>Tournefortia membranacea</i> (3), <i>Eugenia uniflora</i> (3)	23	51.1		
Maia 2001	Southeast	RJ	Atlantic Forest	108	53	32	2.04	Burseraceae (8), Nyctaginaceae (5)	Burseraceae (8), <i>Guapira opposita</i> (6), <i>Protium sagittatum</i> (7), <i>Tetragastris panamensis</i> (6), <i>Miconia stenostachya</i> (6)	94	87.0		
Maia 2011	North	PA	Amazon	76	38	22	2.00	Fabaceae (11) e Melastomataceae	Fabaceae (11) e <i>panamensis</i> (6), <i>Copaifera langsdorffii</i> (5)	25	32.9		
Maia 2013	Southeast	MG	Atlantic Forest	152	94	37	1.62	(18), Myrtaceae (17)	Melastomataceae (10), <i>Myrcia sylvatica</i> (7), <i>Calophyllum brasiliense</i> (6)	82	53.9		
Maia 2014	Southeast	MG	Atlantic Forest	101	63	23	1.60	(29), Asteraceae (18), Myrtaceae	Asteraceae sp. 2 (6), <i>Marierea</i> sp. (5) (11)	51	50.5		

TABLE I (continuation)

Inventories	Brazilian regions	Brazilian states	Biomes	Gall-inducing insect richness	Plant species richness	Plant family richness	Number of gall morphotypes per plant species	Number of gall families (number of insect gall morphotypes)	Super-host species (number of insect gall morphotypes)	Richness of Cecidomyiidae	% of Cecidomyiidae
Maia et al. 2008	Southeast	SP	Atlantic Forest	233	123	48	1.89	Asteraceae (29), Melastomataceae (18)	<i>Myrcia fallax</i> (7), <i>Paulinbia</i> sp. (7), <i>Guapira opposita</i> (6)	135	57.9
Maia et al. 2014	Southeast	ES	Atlantic Forest	265	141	49	1.88	Asteraceae (36), Fabaceae (32), Myrtaceae (27)	<i>Inga</i> sp. 1 (10), <i>Myrcia</i> sp. 1 (8), <i>Guapira opposita</i> (8)	129	48.7
Malves and Friero-Costa 2012	Southeast	MG	Cerrado	57	43	18	1.33	Asteraceae (6), Asteraceae (6), Myrtaceae (5), Melastomataceae (3)	<i>Croton</i> sp. (4), <i>Eugenia</i> sp. 2 (3)	14	24.6
Moreira et al. 2007	Southeast	MG	Atlantic Forest	50	41	15	1.22	Fabaceae (8), Bigoniaceae (7), Asteraceae (7)	<i>Vernonia polyanthes</i> (3), <i>Bigoniaceae</i> Sp. 1 (3)	44	88.0
Oliveira and Maia 2005	Southeast	RJ	Atlantic Forest	43	25	19	1.72	Myrtaceae (7), Erythroxylaceae (5)	<i>Erythroxylum ovalifolium</i> (5)	39	90.7
Nogueira et al. 2016	Northeast	BA	Cerrado-Caatinga	49	14	13	3.50	Fabaceae (22), Malpighiaceae (10)	<i>Copaifera langsdorffii</i> (10), <i>Bauhinia acurana</i> (5), <i>Mimosa gemmiflora</i> (4)	9	18.4
Rodrigues et al. 2014	Southeast	RJ	Atlantic Forest	147	70	33	2.10	Myrtaceae (20), Bignoniaceae (13), Fabaceae (11)	<i>Guapira opposita</i> (8), <i>Byrsonima sericea</i> (5)	80	54.4

TABLE I (continuation)

Inventories	Brazilian regions	Brazilian states	Biomes	Gall-inducing insect richness	Plant species richness	Plant family richness	Number of gall morphotypes per plant species	Number of gall families (number of insect gall morphotypes)	Super-host species (number of insect gall morphotypes)	Richness of Cecidomyiidae	Richness of Cecidomyiidae
<i>Byrsinina</i>											
Saito and Urso-Guimarães 2012	Southeast	SP	Cerrado	69	41	24	1.68	(9), Annonaceae (7), Myrtaceae (7)	Malpighiaceae (9), <i>Duguetia furfuracea</i> (5), <i>Arrabidaea</i> sp. (4)	23	33.3
Santos et al. 2010	Midwest	GO	Cerrado	34	20	12	1.70	Fabaceae (9), Myrtaceae (6), Ulmaceae (4)	<i>Inga cylindrica</i> (3), <i>Serjania obusidentata</i> (3), <i>Guapira</i> sp. 1 (7), <i>Nyctaginaceae</i> (15), Fabaceae (10), Meliaceae (8)	13	38.2
Santos et al. 2011a	Northeast	PE	Atlantic Forest	80	49	28	1.63	(15), Fabaceae (10), Meliaceae (8)	<i>Guapira</i> sp. 2 (7), <i>Guarea macrophylla</i> (6)	65	81.3
Santos et al. 2011b	Northeast	PE	Caatinga	64	48	17	1.33	Fabaceae (15), Euphorbiaceae (9)	<i>Bauhinia cheilantha</i> (4)	57	89.1
Santos et al. 2012a	Midwest	GO	Cerrado	56	34	21	1.65	Fabaceae (14), Euphorbiaceae (9)	Fabaceae (15), <i>Vochysiaceae</i> (8), <i>Andira paniculata</i> (5)	18	32.1
Santos et al. 2012b	Northeast	PE	Atlantic Forest	136	79	35	1.72	Malpighiaceae (5)	Malpighiaceae (9), <i>Lecythidaceae</i> (9), Myrtaceae (9), Nyctaginaceae (9)	Guapira opposita (9), <i>Eschweilera ovata</i> (6), <i>Protium heptaphyllum</i> (6), <i>Styrax polhillii</i> (4)	94.9
Silva et al. 2015	Midwest	GO	Cerrado	42	22	20	1.91	Burseraceae (7), Fabaceae (5)	<i>Burseraceae</i> (7), <i>Protium heptaphyllum</i> (7), <i>Siparuna guianensis</i> (4)	6	14.3

TABLE I (continuation)

Inventories	Brazilian regions	Brazilian states	Biomes	Gall-inducing insect richness	Plant species richness	Plant family richness	Number of gall morphotypes per plant species	Super-host families (number of insect gall morphotypes)	Super-host species (number of insect gall morphotypes)	Richness of Cecidomyiidae (gall morphotypes)	% of Cecidomyiidae
Toma and Mendonça Jr 2013	South	RS	Pampas	57	43	18	1.33	Myrtaceae (20), Asteraceae (8), Melastomataceae (5)	Siphoneugena reitzii (4), <i>Myrcia guianensis</i> (3), <i>Ilex microdonta</i> (3)	31	54.4
Urso-Guimarães and Scarcelli-Santos 2006	Southeast	SP	Cerrado	36	26	15	1.39	Fabaceae (7), Myrtaceae (5), Annonaceae (4)	Duguettia furfuracea (3), <i>Myrcia bella</i> (3)	19	52.8
Urso-Guimarães et al. 2003	Southeast	MG	Cerrado	22	19	16	1.16	Fabaceae (5)	No super-host	12	54.5
Urso-Guimarães et al. 2017	Midwest	MS	Cerrado, Atlantic Forest, Pantanal and Chaco					<i>Fridericia chica</i> (7), Fabaceae (34), Sapindaceae (24), Bignoniaceae (17)	<i>Fridericia chica</i> (7), <i>Serjania</i> cf. <i>glabrata</i> (7), <i>Eugenia florida</i> (6)	39	21.0

Legend: AL: Alagoas; AM: Amazonas; BA: Bahia; CE: Ceará; ES: Espírito-Santo; GO: Goiás; MG: Minas Gerais; MS: Mato Grosso do Sul; PA: Pará; PE: Pernambuco; RJ: Rio de Janeiro; RS: Rio Grande do Sul; SE: Sergipe; SP: São Paulo.

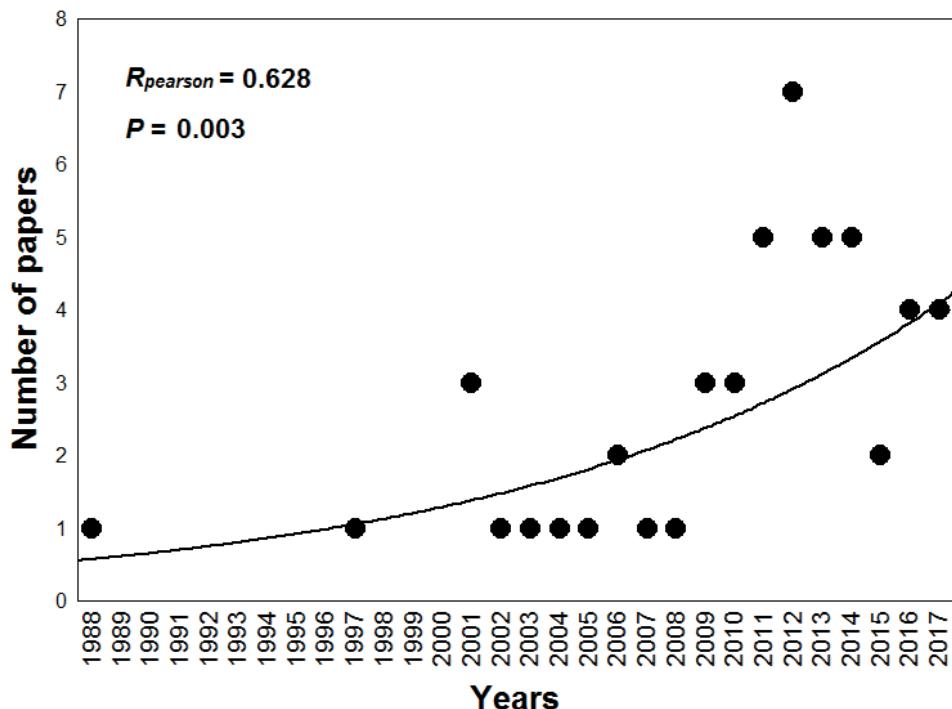


Figure 2 - Temporal trends (1988-2017) in publications on gall-inducing insect inventories performed in Brazil.

A significant geographical bias can be observed among the Brazilian gall-inducing insect inventories. Although inventories have been performed in all the five Brazilian regions, the greatest number has been in the Southeast region (30), with three times the number of studies in the Midwest and Northeast regions (eight studies each). This pattern is due to the Southeast region being the first (chronologically) to be sampled, while at the same time housing the first research centers focusing on gall-inducing insects in Brazil (Universidade Federal de Minas Gerais and Universidade Federal do Rio de Janeiro, respectively). This geographical bias is confirmed by the fact that 33.3% and 19.6% of the published inventories were performed in the states of Minas Gerais and Rio de Janeiro, respectively. The gall-inducing insect diversity of the North and South regions and several Brazilian states remains subsampled or completely unknown.

Most of the Brazilian gall-inducing insect inventories were performed in the Atlantic Forest and Cerrado biomes, which are relevant global biodiversity hotspots (Myers et al. 2000). Estimates indicate that more than 14,000 vascular plant species occur in the Atlantic Forest (Stehmann et al. 2009) and 12,000 in the Cerrado (Mendonça et al. 2008), with these biomes also being considered hotspots of gall-inducing insect diversity (Araújo et al. 2014a, Santos et al. 2014). The Amazon, which is the largest biome in Brazil, had a small number of published studies (4). The same was observed for other Brazilian biomes (e.g., Caatinga, Pampas and Pantanal) that together sum only 12% of the gall-inducing insect inventories in Brazil. Thus, there are still many gaps in the knowledge of gall-inducing insects of Brazil considering both the political (i.e., regions and states) and the ecological (i.e., biomes) organization of the territory.

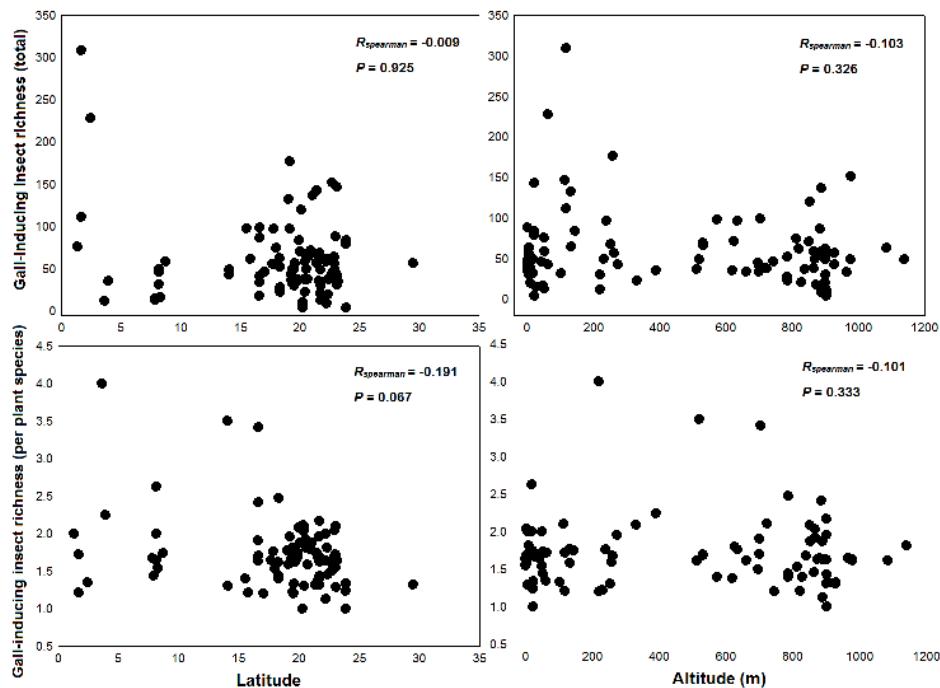


Figure 3 - Effect of latitude and altitude on the gall-inducing insect richness total and per plant species.

Cecidomyiidae (Diptera) was the most important gall-inducing group, producing an average of 63.9% of gall morphotypes of the Brazilian gall-inducing insect inventories. This pattern corroborates the study of Espírito-Santo and Fernandes (2007), which estimated that 64% of gall-inducing insect species in the world belong to the family Cecidomyiidae. In spite of the preponderance of cecidomyiids in Brazilian inventories, they are usually not identified to the species level, either because of taxonomic uncertainties (i.e., difficulties researchers have in determining species) or because they have yet to be described and named (i.e., new species for science). Gagné and Jaschhof (2014), which created a worldwide catalog of cecidomyiids, hypothesize that the number of unidentified Cecidomyiidae species is inestimable, especially in the tropics. Due to the large floristic diversity of Brazilian grasslands, forests and savannas (Forzza et al. 2012), Brazilian biomes are likely to harbor

2004, Bergamini et al. 2017). Myrtaceae was found to be more important in Atlantic Forest inventories (e.g., Rodrigues et al. 2014, Carvalho-Fernandes et al. 2016, Maia and Silva 2016), while Asteraceae was found important in inventories of Atlantic Forest (e.g., Fernandes et al. 2001, Maia et al. 2014) and Cerrado (Carneiro et al. 2009, Coelho et al. 2013b). The main reason for the great importance of Fabaceae, Myrtaceae and Asteraceae as super-hosts of gall-inducing insects is the high number of species they encompass (Araújo 2011). These families are listed among the top ten richest families of Brazil with nearly 2,700 species in Fabaceae, 1,900 in Asteraceae and 920 in Myrtaceae (BFG 2015). The most important super-host species were *Protiom heptaphyllum* (Burseraceae) and *Copaifera langsdorffii* (Fabaceae). Both these species are widely distributed throughout Brazil (Lorenzi 1992), which can be explained by the high number of local gall morphospecies recorded by each particular gall-inducing insect inventory (i.e.,

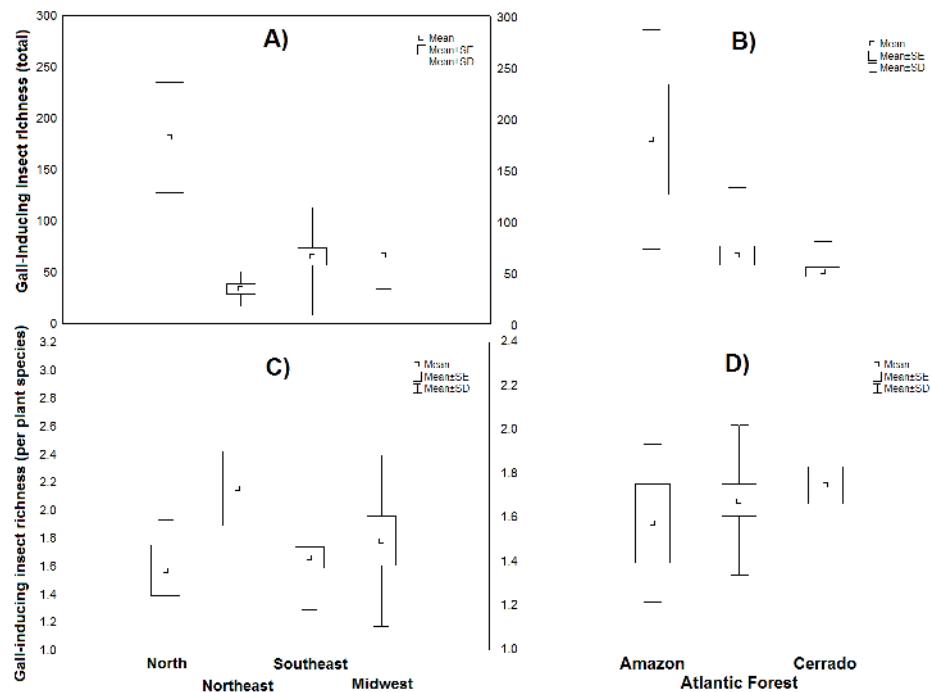


Figure 4 - Comparison of the gall-inducing insect richness total and per plant species between different regions and biomes in Brazil.

the highest diversity of gall-inducing insects in the world (Espírito-Santo and Fernandes 2007). For this reason, in addition to making inventories, it is extremely important to refine the taxonomic understanding of galling insect groups. In this sense, there is an urgent need for investments to increase the number of taxonomists, particularly in Brazil where there is already a deficit of taxonomists specializing on galling insects.

A consistent pattern observed among the inventories of gall-inducing insects in Brazil is that Fabaceae, Myrtaceae and Asteraceae are the most important host plant families. In virtually all compiled inventories at least one of these families appears in the top three most important families (see Table I). The importance of Fabaceae was found to be true for many Brazilian biomes, such as the Amazon (e.g., Almada et al. 2011, Araújo et al. 2012), Atlantic Forest (e.g., Fernandes and Negreiros 2006, Maia and Carvalho-Fernandes 2016), Caatinga (e.g., Santos et al. 2011b, Costa et al. 2014) and Cerrado (e.g., Maia and Fernandes

alpha diversity) as well as regional richness (i.e., beta diversity) (Araújo et al. 2013). Other factors, such as architecture, phenology and release of natural enemies, can also explain the importance of these plant species to host galling insects (Araújo et al. 2013).

Another interesting pattern obtained from the inventories of insect galls in Brazil is that the total richness of gall-inducing insects differs among sampling sites of different Brazilian regions and biomes, but the same is not true for the number of gall morphotypes per plant species. The gross number of gall-inducing insects recorded at the sampling sites in the North region and Amazon biome were much higher than at other Brazilian sites. This result can be explained by the high plant species richness in tropical rain forests and the great environmental stress on the forest canopy (Julião et al. 2014), in addition to sampling factors (i.e., different sampling efforts and methodologies). On the other hand, when controlling for differences in host plant richness (and, consequently, sampling

differences too) by using the number of gall-inducing insects per host plant species, these differences disappear. This result confirms previous studies that pointed out that local and regional difference in the plant species richness are the main factors that explain the richness of galling insects (Cuevas-Reyes et al. 2004, Araújo et al. 2014b, Araújo 2017). The number of gall-inducing insect morphotypes per plant species varied relatively little, being on average 1.72 (± 0.43) gall morphotypes per plant species in Brazilian inventories. Other possible explanatory factors, such as latitude, elevation and vegetation type, were not found to influence the diversity of gall-inducing insects in Brazil. This absence of effects may be due to other non-controlled characteristics of the sampling sites, such as vegetation structure and conservation status.

This study represents the first systematic compilation of inventories of gall-inducing insects in Brazil. Given the growing interest in this line of research, as evidenced by the recent significant increase in the number of publications on the subject, this study identifies the main trends and gaps in the knowledge of gall-inducing insects in Brazil. Based on the results obtained, it is clear that sampling efforts by cecidologists are needed in less studied regions of Brazil, especially the North and South regions and subsampled biomes such as Amazon, Caatinga, Pampas and Pantanal. Furthermore, investment in the production of new taxonomists specializing on galling insects is urgently needed, particularly for Cecidomyiidae, in order to improve the taxonomic resolution of the surveys that have been carried out. Finally, the results presented herein emphasize the importance for cecidologists to publish their inventories in scientific journals. In addition to the acquisition of basic knowledge related to the description of group diversity, these surveys are vital to applied research, such as serving as indicator species or being used in testing ecological hypotheses.

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AUTHOR CONTRIBUTIONS

W.S.A. conceived of the presented idea and compiled the database. W.S.A., G.W.F. and J.C.S. discussed the results and wrote the manuscript.

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