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CONTRIBUTION TO THE KNOWLEDGE OF GALL-INDUCING INSECTS IN THE AMAZON FOREST

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ABSTRACT

Little is known about galling insects in the Amazonian rainforest, despite its renown as a highly biodiverse ecosystem. In an effort to fill this knowledge gap, we compiled data from existing studies of gall-inducing insects and their host plants in the Amazon biome. A total of 32 studies focusing on insect galls and their host plants in the Amazon were assessed. Taxonomy, inventory, and ecology emerged as the most prominently represented areas of investigation. We found 31 species of Cecidomyiidae, from seven tribes and 21 genera, reported in the Amazon Forest. The richness of gall-inducing insects exhibited a positive correlation with the size of their associated plant families, while showing no significant correlation with the age of those families.

KEYWORDS: Cecidomyiidae, host plant, insect galls, insect-plant interaction, rainforesty

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CONTRIBUCIÓN AL CONOCIMIENTO DE LOS INSECTOS INDUCTORES DE AGALLAS EN EL BOSQUE AMAZÓNICO

RESUMEN

Se conoce poco sobre los insectos agalladores en el bosque amazónico, a pesar de su fama como un ecosistema altamente biodiverso. En un esfuerzo por llenar esta brecha de conocimiento, compilamos datos de estudios existentes sobre insectos inductores de agallas y sus plantas hospederas en el bioma amazónico. Se evaluaron un total de 32 estudios que se enfocaban en agallas de insectos y sus plantas hospederas en la Amazonia. Taxonomía, inventario y ecología surgieron como las áreas de investigación más prominentemente representadas. Encontramos 31 especies de Cecidomyiidae, de siete tribus y 21 géneros, reportadas en el bosque amazónico. La riqueza de los insectos inductores de agallas exhibió una correlación positiva con el tamaño de sus familias de plantas asociadas, mientras que no mostró una correlación significativa con la edad de esas familias.

PALABRAS CLAVE: Cecidomyiidae, planta hospedera, agallas de insectos, interacción insecto-planta, bosque tropical

INTRODUCTION

Galls are abnormal growths of plant cells, tissues, or organs formed by hyperplasia (increase in the number of cells) and/or hypertrophy (increase in cell size); they can be induced by an array of agents—including fungi, viruses, bacteria, nematodes, mites, and insects (Fernandes *et al.*, 2012). Among these gall-inducing organisms, insects account for the greatest diversity of galls (Ozaki *et al.*, 2007; Grandez-Rios *et al.*, 2015; Miller III & Raman, 2019). Six insect orders include gall-inducing species: Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, and Thysanoptera (Nieves-Aldrey, 1998; Shorthouse *et al.*, 2005; Coutinho *et al.*, 2019, Araújo *et al.*, 2021). However, the Cecidomyiidae (Diptera) are the most common gall inducer in all zoogeographical regions (Gagné & Jaschhof, 2021). These insects can induce galls on any part of the plant, including both vegetative and reproductive organs, but are most prevalent in leaves and stems (Mani, 1964; Bergamini *et al.*, 2017; Araújo *et al.*, 2021; Flor *et al.*, 2022). Gall-inducing insects are considered the most specialized herbivores on the planet, exhibiting high specificity to their host plants (Carneiro *et al.*, 2009; Araújo, 2013a; Araújo *et al.*, 2017). The most of cecidogenic species induces a unique gall morphotype on the host plant, with the gall considered the extended phenotype of the inducing insect (Stone & Schönrogge, 2003).

The Amazon rainforest is the world's largest tropical forest, covering an area of 7.5 million km2 across nine South American countries. Brazil has the largest area of the forest, accounting for 60% of this vast area, followed by Peru with 13%. The other countries sharing the Amazon have smaller extents, including Colombia, Bolivia, Ecuador, French Guiana, Guyana, Suriname, and Venezuela (Silva-Souza & Souza, 2020). This forest holds 20% of the planet's freshwater supply, significant carbon reserves, and a vast diversity of flora and fauna. It is estimated that the Amazon harbors at least 25% of the planet's biodiversity, with about 50,000 plant species and 2.5 million insect species. However, despite the extraordinarily high plant diversity only 2% of known Cecidomyiidae species come from the Amazon (Julião, 2007).

Reports of insect galls in the Amazon date back to the early 20th century. The first studies were published by notable taxonomists such as Rübsaamen (1905, 1915a, 1915b), Felt (1915, 1921), and Kieffer (1913), who described a large number of gall-inducing insect species in this biome (Maia, 2021). Additionally, a study by Berlin & Prance (1978) reported that the Aguaruna tribe in the Peruvian Amazon used galls from the plant species Moquilea cecidiophora (Prance) Sothers & Prance (Chrysobalanaceae) to make necklaces for decoration. Very little was added to this body of knowledge until the early 21st century, when a resurgence of interest in galling insects among Brazilian workers prompted several wide-ranging studies (Araújo, 2018). These took various approaches to the topic, variously focusing on inventories, taxonomy or ecology (e.g., Maia & Vásquez, 2006; Maia, 2011; Julião *et al.*, 2014). Nevertheless, the Amazon remains one of the least studied biomes in the Neotropical region.

Various hypotheses have been proposed to explain patterns of gall-inducing insect richness (Fleck & Fonseca, 2007). Some consider the possibility that plant diversity influences gall diversity both temporally and spatially. These include the “plant taxon size hypothesis” and the “plant taxon age hypothesis” (Fernandes, 1992). The first predicts that more diverse host taxa should have higher gall richness, considering each host species as a potential niche for insects (Mendonça, 2007). The second hypothesis proposes that older host taxa should have more gall-inducing species, as longer evolutionary time leads to more speciation events (Fernandes, 1992).

Existing studies have contributed to the understanding of gall diversity and the ecology of interactions between gall-inducing insects and host plants in the Amazon. This study aims to identify the principal topics in the study of gall insects and their associated host plants, and to test the taxon size and plant taxon age hypotheses in the Amazon. In order to do that, we analyze the correlations between gall-inducing insect richness and the size and age of their host taxa.

MATERIALS AND METHODS

The study was conducted through a survey of data on gall-inducing insects and their host plants in the Amazon, available on scientific databases. Articles were searched using the online databases SciVerse Scopus, Portal Capes, and Google Scholar between June and July 2023, using the following keyword combinations: (galls* OR insect galls*) AND (Cecidomyiidae*) AND (Amazon*) AND (rainforest*). Data from master's dissertations and doctoral theses were included only when it was explicitly indicated that the study was conducted in the Amazon.

Data from inventories of gall-inducing insects and their host plants in the Amazon forest were obtained from papers published up until 2023. These studies compiled all published surveys for the Amazon that included taxonomic information on host plants and gall-inducing insects, totaling seven articles (Supplementary Material 1). Additionally, all information obtained underwent rigorous review, including verification of botanical names and synonyms, as well as detailed revision of gall and inducer morphology. Botanical families were updated according to the classification system proposed in APG IV (2016). The number of species in each family was checked on the APG website (Stevens, 2001; APG IV, 2016). The age of families in the orders Malpighiales and Myrtales were obtained from Xi *et al.* (2012) and Berger *et al.* (2016), respectively, while the age of the Connaraceae and Siparunaceae families was extracted from Baas *et al.* (2017) and Renner, 2004, respectively. For the remaining families, Wikström *et al.* (2001) was used.

All compiled studies were categorized based on the topic or field of knowledge to which they were most related, according to the title and abstract (or full text if necessary). Topics included: ecology (investigation of ecological factors at the population, community, or biogeographical level); inventory (lists of galls and host plants); taxonomy (systematics, species descriptions, and reviews of gall-inducing species); conservation (habitat restoration and bioindicators of habitat quality); and ethnobotany (human-plant interaction through ancestral knowledge).

To relate the richness of gall-inducing insects to the size and age of the plant taxon, Spearman correlations were used, because the distribution of residuals did not follow a normal distribution when analyzed by the Shapiro-Wilk test. The analyses were performed using the R software version 4.3.1 (R Core Team, 2023), using the cor.test function from the pspearman package.

RESULTS

A total of 32 articles (Supplementary Material 1) on insect galls and their host plants in the Amazon were compiled, covering various topics (Figure 1). Among them, taxonomy (13 articles), inventory (n = 9), and ecology (n = 7) were the most frequent, collectively representing 91% of all publications. The topics of the remaining articles were conservation (n = 2) and ethnobotany (n = 1). Despite an extensive search for publications in different databases, articles were found only for areas of the Amazon rainforest in Brazil (n = 30) and Peru (n = 2), with no publications on the subject for the other countries where this biome extends.

In total, 31 species of Cecidomyiidae from seven tribes and 21 genera were reported in the Amazon (Table 1). The best-represented tribes were Lopesiini and Asphondyliini, each with seven species. The other tribes had lower values: Clinodiplosini (four); and Anadiplosini, Alycaulini, Cecidomyiini, and Dasineurini, each with one specie.

Plants in the orders Malpighiales, Fabales, and Sapindales hosted the highest number of galling insect taxa: 180 morphotypes in Malpighiales; 156 in Fabales; and 154 in Sapindales. “Superhost” families included Fabaceae (153 morphotypes); Burseraceae (89); Bignonaceae (58); Sapotaceae (43); and Lauraceae (37) (Table 2).

The richness of gall-inducing insects ranged from 1 to 153, as assessed by gall morphotypes. Richness was positively correlated with the size of the plant family in terms of species number (RSpearman = 0.30, n = 68, p = 0.0127, Figure 2a). However, the age of botanical families was not correlated with the richness of gall-inducing insects (p = 0.90, Figure 2b).

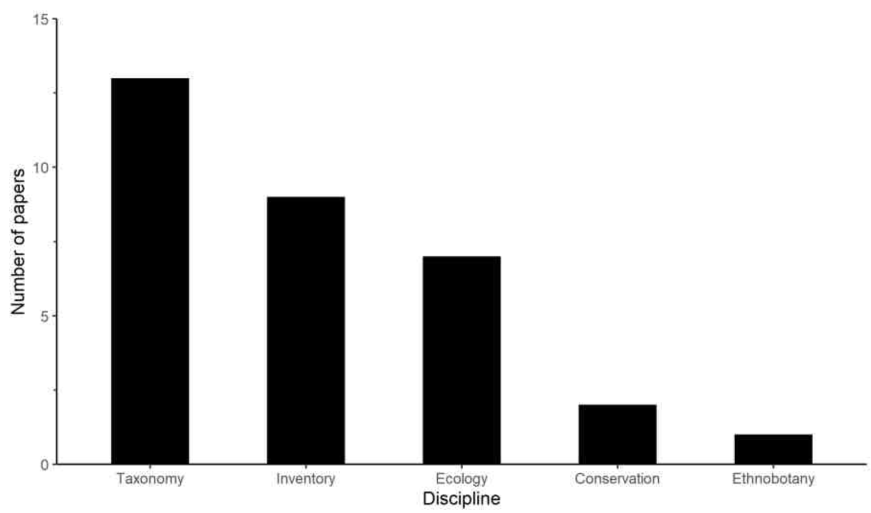

Figure 1. Number of publications about insect galls reported in the Amazon, arranged by area of knowledge.

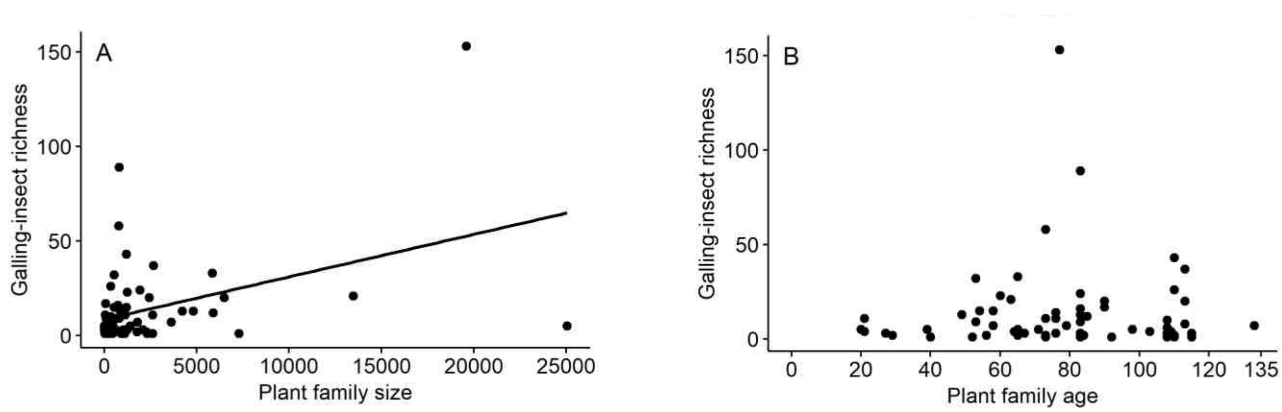

Figure 2. Effects of A) host plant family size (number of species) and B) host plant family age (in millions of years) on the richness of gall-inducing insects in the Amazon forest.

Table 1. Gall-inducing insect species of the family Cecidomyiidae (Diptera) reported for the Amazon forest. The hyphen indicates species not placed in a tribe.

Tribe	Cecidomyiidae genera	Cecidomyiidae species
Alycaulini	*Alycaulus*	*Alycaulus mikaniae* Rübsaamen, 1915a
Anadiplosini	*Alexomyia*	*Alexomyia ciliata* Felt, 1921
Asphondyliini	*Asphondylia*	*Asphondylia fructicola* Maia, 2009
Asphondyliini	*Asphondylia*	*Asphondylia tournefortiae* Rübsaamen, 1915a
Asphondyliini	*Bruggmannia*	*Bruggmannia depressa* Kieffer, 1913
Asphondyliini	*Bruggmannia*	*Bruggmannia longiseta* Kieffer, 1913
Asphondyliini	*Macroporpa*	*Macroporpa peruviana* Rübsaamen, 1915a
Asphondyliini	*Macroporpa*	*Macroporpa ulei* Rübsaamen, 1915b
Asphondyliini	*Perasphondylia*	*Perasphondylia reticulata* Möhn, 1960
Cecidomyiini	*Contarinia*	*Contarinia gemmae* Maia, 2003
Clinodiplosini	*Clinodiplosis*	*Clinodiplosis cecropiae,* Proença & Maia 2020
Clinodiplosini	*Clinodiplosis*	*Clinodiplosis eupatorii* Felt, 1911
Clinodiplosini	*Iatrophobia*	*Iatrophobia brasiliensis* Rübsaamen, 1908
Clinodiplosini	*Schismatodiplosis*	*Schismatodiplosis lantanae* Rübsaamen, 1908
Dasineurini	*Dasineura*	*Dasineura theobromae* Maia, 2006
Lopesiini	*Lopesia*	*Lopesia aldinae* Fernandes & Maia, 2010
Lopesiini	*Lopesia*	*Lopesia caulinaris* Maia, 2003
Lopesiini	*Lopesia*	*Lopesia conspicua* Maia, 2003
Lopesiini	*Lopesia*	*Lopesia similis* Maia, 2004
Lopesiini	*Lopesia*	*Lopesia elliptica* Maia, 2003
Lopesiini	*Lopesia*	*Lopesia linearis* Maia, 2003
Lopesiini	*Lopesia*	*Lopesia maricaensis* Rodrigues & Maia, 2010
-	*Frauenfeldiella*	*Frauenfeldiella coussapoae* Rübsaamen, 1905
-	*Haplopalpus*	*Haplopalpus serjaneae* Rübsaamen, 1915b
-	*Haplusia*	*Haplusia braziliensis* Felt, 1915
-	*Megaulus*	*Megaulus sterculiae* Rübsaamen, 1915b
-	*Ouradiplosis*	*Ouradiplosis aurata* Felt, 1915
-	*Parkiamyia*	*Parkiamyia paraensis* Maia, 2006
-	*Uleia*	*Uleia clusiae* Rübsaamen, 1905
-	*Heterodiplosis*	*Heterodiplosis peruviana* Maia, 2010
-	*Dactylodiplosis*	*Dactylodiplosis heisteriae* Rübsaamen, 1915b

Table 2. Number of plant species, plant genera and galling insect species recorded for different host plant families and orders in the Amazon. Family size obtained from Stevens (2001).

Order	Family	Number of plant species	Number of plant genera	Galling-insect richness
Fabales	Fabaceae	19,580	766	153
Sapindales	Burseraceae	818	19	89
Lamiales	Bignoniaceae	790	110	58
Ericales	Sapotaceae	1,188	53	43
Laurales	Lauraceae	2,675	50	37
Myrtales	Melastomataceae	5,858	176	33
Malpighiales	Chrysobalanaceae	530	18	32
Ericales	Lecythidaceae	353	25	26
Sapindales	Sapindaceae	1,925	144	24
Malpighiales	Malpighiaceae	1,250	68	23
Gentianales	Rubiaceae	13,465	614	21
Magnoliales	Annonaceae	2,430	110	20
Malpighiales	Euphorbiaceae	6,499	218	20
Laurales	Siparunaceae	75	2	17
Sapindales	Meliaceae	740	58	16
Malpighiales	Hypericaceae	534	9	15
Malpighiales	Salicaceae	1,200	54	15
Rosales	Moraceae	1,137	39	14
Gentianales	Apocynaceae	4,828	400	13
Malvales	Malvaceae	4,225	243	13
Sapindales	Anacardiaceae	873	80	13
Myrtales	Myrtaceae	5,900	131	12
Malpighiales	Humiriaceae	63	7	11
Rosales	Urticaceae	2,625	54	11
Malpighiales	Violaceae	1,126	34	11
Dilleniales	Dilleniaceae	360	11	10

Table 2. Continue.

Order	Family	Number of plant species	Number of plant genera	Galling-insect richness
Malpighiales	Ochnaceae	650	33	9
Sapindales	Simaroubaceae	110	21	9
Malpighiales	Clusiaceae	800	14	9
Magnoliales	Myristicaceae	503	20	8
Boraginales	Boraginaceae	1,793	94	7
Malpighiales	Calophyllaceae	460	13	7
Piperales	Piperaceae	3,615	5	7
Caryophyllales	Nyctaginaceae	405	32	6
Asterales	Asteraceae	25,040	1620	5
Myrtales	Vochysiaceae	250	8	5
Oxalidales	Connaraceae	180	12	5
Malpighiales	Lacistemataceae	17	2	5
Celastrales	Celastraceae	1,410	94	5
Malpighiales	Peraceae	135	5	4
Malpighiales	Goupiaceae	2	1	4
Myrtales	Combretaceae	500	10	4
Malpighiales	Dichapetalaceae	165	3	4
Fabales	Polygalaceae	1,236	29	3
Malpighiales	Passifloraceae	1,035	27	3
Santalales	Coulaceae	3	3	3
Oxalidales	Elaeocarpaceae	635	12	3
Ranunculales	Menispermaceae	442	71	3
Rosales	Cannabaceae	117	10	3
Icacinales	Icacinaceae	178	23	3
Sapindales	Rutaceae	2,085	161	3
Santalales	Erythropalaceae	40	4	3
Solanales	Solanaceae	2,280	102	2

Table 2. Continue.

Order	Family	Number of plant species	Number of plant genera	Galling-insect richness
Solanales	Convolvulaceae	1,770	59	2
Ericales	Ebenaceae	855	4	2
Malpighiales	Erythroxylaceae	240	4	2
Malpighiales	Achariaceae	133	30	2
Malpighiales	Caryocaraceae	27	2	2
Lamiales	Verbenaceae	775	32	2
Ericales	Primulaceae	2,615	58	1
Caryophyllales	Polygonaceae	1,115	55	1
Santalales	Loranthaceae	930	77	1
Aquifoliales	Aquifoliaceae	453	1	1
Malpighiales	Linaceae	268	7	1
Liliales	Smilacaceae	233	1	1
Malvales	Bixaceae	21	4	1
Lamiales	Lamiaceae	7,280	236	1
Malpighiales	Phyllanthaceae	2,330	66	1

DISCUSSION

With respect to the areas of knowledge covered in the studies, taxonomy constitutes 41% of all publications, playing a fundamental role in describing the diversity of gall-inducers—especially within the Cecidomyiidae family, which is the most relevant group of gall-inducing insects in the Neotropical region and worldwide (Gagné & Jaschhof, 2021). Inventories accounted for 28% of the compiled articles; these focused on the occurrence and morphological characterization of insect galls, with notes on host plants and vegetation types in different regions. These studies are crucial for describing the diversity of insect galls in various locations and providing relevant information for the development of other research lines (Araújo, 2018). Although inventories of insect galls have been conducted in various vegetation types and geographic regions, large areas remain unexplored or unsampled. This leads to an underestimation of the diversity of insect galls present in the Amazon.

Additional important theme in study on insect galls in the Amazon included the field of ecology, which accounted for 22% of the publications. These included studies addressing patterns of diversity among gall-inducing insects as a function of floristic diversity (plant richness hypothesis), as well as structural characteristics of vegetation (vertical stratification hypothesis) and aspects of the physical environment (hygrothermal stress hypothesis) (Fleck & Fonseca, 2007).

In relation to the ecological patterns tested in this study, the hypothesis that host plant taxon size is a determinant of galling insect richnes was broadly supported, as the number of galling species observed in a host plant family was positively correlated with the taxonomic richness of that family. It is important to emphasize that this pattern was strongly influenced by the Fabaceae family (excluding this family, the correction is not significant). This pattern has also been seen in habitats outside the Amazon, including the Cerrado (Araújo *et al.*, 2013b), Atlantic forest (Fernandes *et al.*, 2001), rocky fields (Coelho *et al.*, 2013), deciduous seasonal forests (Coelho *et al.*, 2009), and subtropical forests (Mendonça, 2007). For instance, Gonçalves-Alvim & Fernandes (2001) found higher species richness of gall-inducing insects among plant families with a larger number of species in the Brazilian Cerrado. In that study, the size of host plant families explained 50% of the variation in gall-inducing insect species richness. Fabaceae, Asteraceae, Myrtaceae, Malpighiaceae, and Erythroxylaceae hosted about 65% of identified gall-inducing insect species. In another study, the number of gall-inducing insects increased with the size of the plant family in the Atlantic forest. In that case, Asteraceae and Melastomataceae were the most important botanical families, together accounting for 44% of gall-inducing insect species richness (Flor *et al.* 2022). These results suggest that species-rich plant families provide more niches for gall forming taxa (Mendonça, 2007).

In contrast to taxon size, taxon age was not a good predictor of gall-inducing insect diversity in the Amazon. Evolutionarily older families did not exhibit greater diversity of gall-inducing insects. Similar results were reported by Araújo (2011) from Brazilian cecidomyiids. Contrary to the predictions of the plant taxon-age hypothesis, relatively young families, such as Fabaceae and Burseraceae, showed higher diversity of gall-inducing insects than older taxa in the Amazon. This may be attributed to the adaptive opportunism of gall-inducing insects. These insects can be found across many host plant families. For instance, gall-inducing genera like Dasineura and Asphondylia have been recorded in 85 plant families in the neotropical region (Price, 2005). Host-switching seems to be favored in more species-rich plant families—likely because species in those families are more recently diverged, and exhibit similar chemical- and phenological characteristics. Considering that gall-inducing insects exhibit host organ specificity and depend on the occurrence of specific hosts for gall induction, a higher number of species within a host taxon increases the likelihood of synchronous development. This may provide greater opportunity for speciation through host-switching (Araújo & Santos, 2009; Flor *et al.*, 2020).

CONCLUSION

The present study documents that some well-studied topics, especially related to the taxonomy, inventory, and ecology of gall-inducing insects, have contributed to the description and explanation of diversity patterns of gall-inducing insects in the Amazon forest. The results obtained also reinforce the importance of taxon size hypotheses in the diversity of gall-inducing insects in the Amazon forest, but not for the age of the plant taxon. Furthermore, it highlights the need to expand studies to improve our understanding of gall-inducing insect diversity across the Amazon biome.

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REFERENCES

APG IV. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society*, 181 (1), 1–20.

Araújo, W.S.; Santos, B.B. 2009. Efeitos da sazonalidade e do tamanho da planta hospedeira na abundância de galhas de Cecidomyiidae (Diptera) em Piper arboreum (Piperaceae). *Revista Brasileira de Entomologia*, 53, 300–303.

Araújo, W.S. 2011. Size, age and composition: characteristics of plant taxa as diversity predictors of gall-midges (Diptera: Cecidomyiidae). *Revista de Biología Tropical*, 59 (4), 1599–1607.

Araújo, W.S. 2013a. Different relationships between galling and non-galling herbivore richness and plant species richness: a meta-analysis. *Arthropod-Plant Interactions*, 7, 373–377.

Araújo, W.S.; Silva, I.P.A.; Santos, B.B.; Gomes-Klein, V.L. 2013b. Host plants of insect-induced galls in areas of cerrado in the state of Goiás, Brazil. *Acta Botanica Brasilica*, 27, 537–542.

Araújo, W.S.; Grandez-Rios, J.M.; Bergamini, L.L.; Kollár, J. 2017. Exotic species and the structure of a plant-galling network. *Network Biology*, 7, 21– 32.

Araújo, W.S. 2018. 30 years of research on insect galls in Brazil: a scientometric review. *Papéis Avulsos de Zoologia*, 58, e20185834.

Araújo, W.S.; Urso-Guimarães, M.V.; Mendonça, M.S.; Santos, J.C. 2021. Sampling Galls and Galling Arthropods. In: Santos, J.C.; Fernandes, G.W. (Eds.). *Measuring Arthropod Biodiversity.*Cham, Springer. p. 403-437.

Baas, P.; Manchester, S.R.; Wheeler, E.A.; Srivastava, R. 2017. Fossil wood with dimorphic fibers from the Deccan Intertrappean Beds of India–the oldest fossil Connaraceae?. *IAWA journal*, 38 (1), 124–133.

Bergamini, B.A.R.; Bergamini, L.L.; Santos, B.B.; Araújo, W.S. 2017. Occurrence and characterization of insect galls in the Floresta Nacional de Silvânia, Brazil. *Papéis Avulsos de Zoologia,* 57, 413–431.

Berger, B.A.; Kriebel, R.; Spalink, D.; Sytsma, K.J. 2016. Divergence times, historical biogeography, and shifts in speciation rates of Myrtales. *Molecular Phylogenetics and Evolution*, 95, 116–136.

Berlin, B.; Prance, G.T. 1978. Insect galls and human ornamentation: The ethnobotanical significance of a new species of Licania from Amazonas, Peru. *Biotropica*, 81–86.

Cardoso, D.; Särkinen, T.; Alexander, S.; Amorim, A.M.; Bittrich, V.; Celis, M.; Daly, D.C.; Fiaschi, P.; Viana, P.L.; Stehmann, J.R.; Van der Werff, H.; Zartman, C.E.; Rapini, A.; Mitchell, J.; Mori, S.A.; Taylor, C.M.; Giacomin, L.L.; Knapp, S.; Forzza, R.C.; Santos, R.M.; Pirani, J.R.; Cavalcante de Lima, H.; Prance, G.T.; Roque, N.; Machado, A.F.P.; Iganci, J.; Moraes, P.L.R.; Moonlight, P.; Kelloff, C.L.; Pennington, T.D.; Heiden, G.; Nunes, T.S.; Shimizu, G.; Goldenberg, R.; Michelangeli, F.A.; Mello-Silva, R.; Sobral, M.; Trovó, M.; Queiroz, L.P.; Van den Berg, C.; Rincon, C.A.V.; Funk, V.A.; Riina, R.; Stevens, W.D. 2017. Amazon plant diversity revealed by a taxonomically verified species list. *Proceedings of the National Academy of Sciences*, 114 (40), 10695–10700.

Carneiro, M.A.A.; Branco, C.S.; Braga, C.E.; Almada, E.D.; Costa, M.; Maia, V.C.; Fernandes, G.W. 2009. Are gall midge species (Diptera, Cecidomyiidae) host-plant specialists?. *Revista Brasileira de Entomologia*, 53, 365–378.

Coelho, M.S.; Almada, E.D.; Fernandes, G.W.; Carneiro, M.A.A.; Santos, R.M.D.; Quintino, A.V.; Sanchez-Azofeifa, A. 2009. Gall inducing arthropods from a seasonally dry tropical forest in Serra do Cipó, Brazil. *Revista Brasileira de Entomologia*, 53, 404–414.

Coelho, M.S.; Carneiro, M.A.A.; Branco, C.; Borges, R.A.X.; Fernandes, G.W. 2013. Gall-inducing insects from Campos de Altitude, Brazil. *Biota Neotropica*, 13, 139–151.

Coutinho, R.D.; Cuevas-Reyes, P.; Fernandes, G.W.; Fagundes, M. 2019. Community structure of gall-inducing insects associated with a tropical shrub: regional, local and individual patterns. *Tropical Ecology*, 60, 74–82.

Felt, E.P. 1915. New South American gall midges. *Psyche*, 22, 152–157.

Felt, E.P. 1921. Three new sub-tropical gall midges (Itonididae, Dipt.). *Entomological News*, 32, 141–143.

Fernandes, G.W. 1992. Plant family size and age effects on insular gall-forming species richness. *Global Ecology and Biogeography Letters*, 2, 71–74.

Fernandes, G.W.; Julião, G.R.; Araújo, R.C.; Araújo, S.C.; Lombardi, J.A.; Negreiros, D.; Carneiro, M.A.A. 2001. Distribution and morphology of insect galls of the Rio Doce Valley, Brazil. *Naturalia*, 26, 211–244.

Fernandes, G.W.; Carneiro, M.A.; Isaias, R.M. 2012. Gall-inducing insects: From anatomy to biodiversity. In: Panizzi, A.R.; Parra, J.R.P. (Eds), *Insect Bioecology and Nutrition for Integrated Pest Management*, CRC Press: Boca Raton, FL, USA, 2014, p. 369–395.

Fleck, T.; Fonseca, C.R. 2007. Hipóteses sobre a riqueza de insetos galhadores: uma revisão considerando os níveis intra-específico, interespecífico e de comunidade. *Neotropical Biology and Conservation*, 2 (1), 36–45.

Flor, I.C.; Maia, V.C.; Carneiro, M.A.A. 2022. Geographic distribution patterns of galling insects in a protected area of Atlantic forest (southeast, Brazil). *Papéis Avulsos de Zoologia*, 62, e202262025.

Gagné, R.J.; Jaschhof, M. 2021. *A Catalog of the Cecidomyiidae (Diptera) of the World*. 5th Edition. Systematic Entomology Laboratory, Agricultural Research Service, U.S. Department of Agriculture U.S. National Museum NHB, Washington, D.C. USA.

Gonçalves-Alvim, S.J.; Fernandes, G.W. 2001. Biodiversity of galling insects: historical, community and habitat effects in four neotropical savannas. *Biodiversity & Conservation*, 10, 79–98.

Grandez-Rios, J.M.; García-Villacorta, R.; Cuevas-Reyes, P.; Araújo, W.S. 2015. Insectos inductores de agallas en América Latina: ecología, importancia y nuevas perspectivas. *Revista de Biologia Neotropical*, 12 (2), 92–103.

Julião, G.R. 2007. *Riqueza e abundância de insetos galhadores associados ao dossel de florestas de terra firme, várzea e igapó da Amazônia Central.* Tese de Doutorado. Universidade Federal do Amazonas, Manaus, 144 pp.

Julião, G.R.; Venticinque, E.M.; Fernandes, G.W.; Price, P.W. 2014. Unexpected high diversity of galling insects in the Amazonian upper canopy: the savanna out there. *PLoS One*, 9 (12), e114986.

Maia, V.C.; Vásquez, J. 2006. A new species of gall midge (Diptera: Cecidomyiidae) associated with Theobroma bicolor (Sterculiaceae) from Peru. *Arquivos do Museu Nacional*, 64 (2), 125–129.

Maia, V.C. 2011. Characterization of insect galls, gall makers, and associated fauna of Platô Bacaba (Porto de Trombetas, Pará, Brazil). Biota Neotropica, 11 (4), 37–53.

Maia, V.C. 2021. Cecidomyiidae (Diptera, Insecta): richness of species and distribution in Brazil. *Biota Neotropica*, 21 (2),

e20201038.
Mani, M.S. 1964. *Ecology of Plant Galls*. Springer, New York, 434 pp.
Mendonça, M.S. 2007. Plant diversity and galling arthropod diversity searching for taxonomic patterns in an animal-plant interaction in the neotropics. *Boletin de la Sociedad Argentina de Botanica*, 42 (3–4), 347–57.
Miller III, D.G.; Raman, A. 2019. Host–plant relations of gall-inducing insects. *Annals of the Entomological Society of America*, 112 (1), 1–19.
Nieves-Aldrey, J.L. 1998. Insectos que inducen la formación de agallas en las plantas: una fascinante interacción ecológica y evolutiva. *Boletín de la Sociedad Entomológica Aragonesa*. 23, 3–12
Ozaki, K.; Yukawa, J.; Ohgushi, T.; Price, P.W. 2006. *Galling arthropods and their associates. Ecology and Evolution*, Springer-Verlag, Tokyo, Japan, 308 pp.
Price, P.W. 2005. Adaptive radiation of gall-inducing insects. *Basic and Applied Ecology,* 6 (5), 413–421.
R Core Team. 2023. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Version 4.3.1.
Renner, S.S. 2004. Variation in diversity among Laurales, Early Cretaceous to present. *Biologiske Skrifter Det Kongelige Danske Videnskabernes Selskab*, 55, 441–458.
Rübsaamen, E.H. 1905. Beitrage zur Kenntnis aussereuropäischer Zoocecidien. II. Beitrag: Gallen aus Brasilien und Peru. (Fortsetzung.). *Marcellia*, 4, 11–138.
Rübsaamen, E.H. 1915a. *Beitrag zur Kenntnis aussereuropäischer Gallmucken*. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 1915, 431–481.
Rübsaamen, E.H. 1915b. *Cecidomyidenstudien V. Revision der deutschen Asphondyliarien*. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 1916, 1–12.
Silva-Souza, K.J.; Souza, A.F. 2020. Woody plant subregions of the Amazon forest. *Journal of Ecology*, 108 (6), 2321–2335.
Shorthouse, J.D.; Wool, D.; Raman, A. 2005. Gall-inducing insects–Nature's most sophisticated herbivores. *Basic and Applied Ecology*, 6 (5), 407–411.
Stevens, P.F. 2001. *Angiosperm Phylogeny Website. Version 13*. (http://www.mobot.org/MOBOT/research/APweb/). (Accessed 12 June 2023).
Stone, G.N.; Schönrogge, K. 2003. The adaptive significance of insect gall morphology. *Trends in Ecology & Evolution*, 18 (10), 512–522.
Wikström, N.; Savolainen, V.; Chase, M.W. 2001. Evolution of the angiosperms: calibrating the family tree. *Proceedings of the Royal Society of London B,* 268, 2211–2220.
Xi, Z.; Ruhfel, B.R.; Schaefer, H.; Amorim, A.M.; Sugumaran, M.; Wurdack, K.J.; Endress, P.K.; Matthews, M.L.; Stevens, P.F.; Mathews, S.; Davis, C.C. 2012. Phylogenomics and a posteriori data partitioning resolve the Cretaceous angiosperm radiation Malpighiales. *Proceedings of the National Academy of Sciences*, 109 (43), 17519–17524.

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Supplementary Material 1. List of references about insect gall and their host plants in the Amazonian rainforest used in this study.

Code	Reference	Discipline
1	Berlin, B.; Prance, G.T. 1978. Insect galls and human ornamentation: The ethnobotanical significance of a new species of Licania from Amazonas, Peru. Biotropica, 81–86.	Ethnobotany
2	Araújo, W.S.; Espírito-Santo Filho, K.; Bergamini, L.L.; Gomes, R.; Morato, S.A.A. 2014. Habitat conversion and galling insect richness in tropical rainforests under mining effect. Journal of insect conservation, 18, 1147–1152.	Conservation
3	Fernandes, G.W.; Almada, E.D.; Carneiro, M.A.A. 2010. Gall-inducing insect species richness as indicators of forest age and health. Environmental entomology, 39(4), 1134–1140.	Conservation
4	Cogni, R; Fernandes, G.W.; Vieira, D.L.M.; Marinelli, C.E.; Jurinitz, C.F.; Guerra, B.R.; Zuanon, J.; Venticinque, E. M. 2003. Galling insects (Diptera: Cecidomyiidae) survive inundation during host plant flooding in Central Amazonia. Biotropica, 35(1), 115–119.	Ecology
5	Fernandes, G.W.; Marco Júnior, P.; Schönrogge, K. 2008. Plant organ abscission and the green island effect caused by gallmidges (Cecidomyiidae) on tropical trees. Arthropod-plant interactions, 2, 93–99.	Ecology
6	Izzo, T.J.; Julião, G.R.; Almada, E. D.; Fernandes, G.W. 2006. Hiding from defenders: localized chemical modification on the leaves of an Amazonian ant-plant induced by a gall-making insect (Diptera: Cecidomyiidae). Sociobiology, 48, 2, 417–426.	Ecology
7	Juliao, G.R.; Venticinque, E.M.; Fernandes, G.W.; Price, P.W. 2014. Unexpected high diversity of galling insects in the Amazonian upper canopy: the savanna out there. Plos one, 9(12), e114986.	Ecology
8	Julião, G.R.; Venticinque, E.M.; Fernandes, G.W. 2018. Influence of flood levels on the richness and abundance of galling insects associated with trees from seasonally flooded forests of Central Amazonia, Brazil. In: Fernandes, G.W.; Santos, J.C. (Eds). Neotropical Insect Galls, Springer Netherlands, Dordrecht, p. 99–117.	Ecology
9	Schwartz, G.; Hanazaki, N.; Silva, M.B.; Izzo, T.J.; Bejar, M.E.; Mesquita, M.R.; Fernandes, G.W. 2003. Evidence for a stress hypothesis: Hemiparasitism effect on the colonization of Alchornea castaneaefolia A. Juss. (Euphorbiaceae) by galling Insects. Acta Amazonica, 33, 275–280.	Ecology
10	Oda, R.A.M. 2008. Distribuição espacial de insetos fitófagos, com ênfase em galhadores, em três diferentes regiões do brasil. Tese doutorado, Rio de Janeiro, Brazil.	Ecology
11	Proença, B.; Maia, C.V. 2023. Insect galls from Amazon rainforest areas in Rondônia (Brazil). Anais da Academia Brasileira de Ciências, 95(4), e20190869.	Inventory
12	Almada, E.D.; Fernandes, G.W.A. 2011. Insetos indutores de galhas em florestas de terra firme e em reflorestamentos com espécies nativas na Amazônia Oriental, Pará, Brasil. Boletim do Museu Paraense Emílio Goeldi-Ciências Naturais, 6(2), 163–196.	Inventory
13	Araújo, W.S.; Porfírio-Júnior, E.D.; Jorge, V.A.; Espírito-Santo, K. 2012. Plantas hospedeiras e galhas entomógenas em sub-bosques de florestas tropicais do Pará, Brasil. INSULA Revista de Botânica, 41, 59–72.	Inventory
14	Carvalho, A.N.; & Mota, J.S. 2018. Ocorrência e caracterização de galhas entomógenas em um fragmento florestal em estágio de sucessão ecológica na Amazônia. EntomoBrasilis, 11(2), 118–123.	Inventory
15	Julião, G.R.; Almada, E.D.; Costa, F.R.C.; Carneiro, M.A.A.; Fernandes, G.W. 2017. Understory host plant and insect gall diversity changes across topographic habitats differing in nutrient and water stress in the Brazilian Amazon rainforest. Acta Amazonica, 47, 237-246.	Inventory
16	Maia, V.C. 2011. Characterization of insect galls, gall makers, and associated fauna of Platô Bacaba (Porto de Trombetas, Pará, Brazil). Biota Neotropica, 11 (4): 37–53.	Inventory
17	Silva, P.S.D.; Almeida-Santos, B.; Tabarelli, M.; Almeida-Cortez, J.S. 2011. Occurrence of gall complexes along a topographic gradient in an undisturbed lowland forest of central Amazonia. Revista Brasileira de Biociências, 9, 133–138.	Inventory

Supplementary Material 1. Continue.

Code	Reference	Discipline
18	Carvalho-Fernandes, S.P. 2010. Insetos galhadores associados à família Burseraceae da Reserva Florestal Ducke, Manaus-AM. Master Thesis, Manaus, Brazil.	Inventory
19	Yukawa, J.; Tokuda, M.; Uechi, N.; Sato, S. 2001. Species richness of galling arthropods in Manaus, Amazon and the surroundings of the Iguassu Falls. Esaki, 41, 11–15	Inventory
20	Rübsaamen, E.H. 1905. Beitrage zur Kenntnis aussereuropäischer Zoocecidien. II. Beitrag:Gallen aus Brasilien und Peru. (Fortsetzung.). Marcellia, 4, 11–138.	Taxonomy
21	Rübsaamen, E.H. 1908. Beiträge zur Kenntnis aussereuropäischer Zoocecidien. III. Beitrag: Gallen aus Brasilien und Peru. Marcellia, 7, 15–79.	Taxonomy
22	Rübsaamen, E.H. 1915a. Beitrag zur Kenntnis aussereuropäischer Gallmucken. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 1915, 431–481.	Taxonomy
23	Rübsaamen, E.H. 1915b. Cecidomyidenstudien V. Revision der deutschen Asphondyliarien. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 1916, 1–12.	Taxonomy
24	Kieffer, J. J. 1913. Diptera. Fam. Cecidomyiidae. Genera Isectorum, 152, 1–346.	Taxonomy
25	Felt, E.P. 1915. New South American gall midges. Psyche, 22, 152–157.	Taxonomy
26	Felt, E.P. 1921. Three new sub-tropical gall midges (Itonididae, Dipt.). Entomological News, 32, 141–143.	Taxonomy
27	Maia, V.C.; Fernandes, G.W. 2006. A new genus and species of gall midge (Diptera, Cecidomyiidae) associated with Parkia pendula (Fabaceae, Mimosoideae). Revista Brasileira de Entomologia, 50, 1–5.	Taxonomy
28	Maia, V.C.; Vásquez, J. 2006 A new species of gall midge (Diptera: Cecidomyiidae) associated with Theobroma bicolor (Sterculiaceae) from Peru. Arquivos do Museu Nacional, 64 (2), 125–129.	Taxonomy
29	Maia, V.C.; Santos, J.C.; Fernandes, G.W. 2009. Asphondylia fructicola, a new species of Cecidomyiidae (Diptera) associated with Solanum sp. (Solanaceae) from Brazil. Revista Brasileira de Entomologia, 53, 166–170.	Taxonomy
30	Maia, V.C.; Vásquez, J. 2010. New genus and species of Cecidomyiidae (Diptera) associated with Arrabidaea sp. (Bignoniaceae) from Peru. Arquivos do Museu Nacional, 68 (1–2), 35–40.	Taxonomy
31	Proença, B.; Maia, V.C. 2020. A new species of Clinodiplosis Kieffer (Diptera, Cecidomyiidae) associated with Cecropia sp. (Urticaceae) in Brazil. Papéis Avulsos de Zoologia, 60, e20206003.	Taxonomy
32	Fernandes, S.P.C.; Maia, V.C.; Rafael, J.A. 2010. Gall midges (Diptera, Cecidomyiidae) associated with Aldina heterophylla Spr. ex Benth. (Fabaceae) from Brazil. Biota Neotropica, 10, 161–166.	Taxonomy