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ECOSYSTEMS

The importance of Brazilian Conservation Units for the diversity of gall-inducing insects: a study on gall-inducing insect richness in the Chapada Diamantina National Park, state of Bahia, Brazil

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Abstract: Conservation Units (CUs) tend to have a high richness of herbivorous insects, including gall-inducing insects. Despite this, gall surveys carried out in these environments are punctual and some units have never had their galls investigated, such as the Chapada Diamantina National Park, Bahia (Chapada Diamantina Parna). Aiming to reduce this gap and contribute to future studies in CUs, this study aimed to survey the galls of the Chapada Diamantina Parna, Lençóis, as well as to investigate trends in research on galls in CUs in Brazil. For that, collections were carried out on monthly trips for one year. Published gall surveys were compiled. A total of 107 morphotypes induced in 88 host species were recorded. Most galls are formed in leaves, globoid in shape, green in color, and induced by Cecidomyiidae. This park has a relatively high richness of galls compared to other CUs, demonstrating its importance in the conservation of gall-inducing insects. The results also revealed that the number of surveys has been increasing over the years and that the Southeast concentrates the largest number of studies, a region that also gathers the largest number of specialists, demonstrating a geographic bias in the data.

Key words: Cecidomyiidae, Fabaceae, Gall-inducing insects-host plant interaction, semiarid.

INTRODUCTION

Preserved environments with high biodiversity tend to have a high richness of herbivorous insects (Root 1973, Fleck & Fonseca 2007). Among the different types of herbivory observed in these environments, the endo-phytophagous habit is considered one of the most threatened by environmental changes, including gall-inducing insects, which are considered the most sophisticated on planet Earth (Shorthouse et al. 2005), as they can induce structures called galls through disordered processes of hyperplasia and/or hypertrophy and cell differentiation in different organs of host plants (Mani 1964, Oliveira & Isaias 2010, Ferreira & Isaias 2013).

The galls provide a microenvironment for the gall-inducing and protect it against abiotic and biotic factors, allowing its success in development and energetic resources for its nutrition (Price et al. 1987, Stone & Schönrogge 2003). On the other hand, plants have their growth and reproduction phase impaired, because, as the galls grow, their nutrients are withdrawn, which can lead to the loss of their branches, fruit, and, in the most severe cases, to death (Price et al. 1987).

Studies on the richness of gall-inducing insects have demonstrated the importance of this insect guild to assess the preservation of the environment (Santos et al. 2012, Santana &

Isaias 2014, Brito et al. 2018). The entomofauna associated with galls respond to environmental disturbances, such as resulting losses of species, richness, and abundance that also impact their natural enemies (Oliveira 2009). Therefore, knowledge about the richness of gall-inducing insects can help in urban planning and management (Julião et al. 2005), in environmental monitoring and conservation (Santana & Isaias 2014, Melo Jr et al. 2018), and also provide broad content for scientific dissemination by involving different scientific concepts and thus being an ally in preservation activities, through the dissemination of data through social media (Santos-Silva & Araújo 2022).

Brazilian Conservation Units (CUs) are protected natural areas that aim to maintain biological diversity in the national territory, including jurisdictional waters, the protection of rare, endemic, vulnerable, or endangered species, and the preservation and restoration of the diversity of natural ecosystems (Law 9985/2000). The number of CUs and the area they protect have been growing in recent decades in Brazil (Drummond et al. 2009). This growth is fundamental and urgent to ensure the conservation of biodiversity, especially in Brazil, which is the fifth largest country in terms of territory in the world, with 8,516,000 km^2, considered to house the greatest biological diversity on the planet, with at least 46,975 native species of algae, fungi, and plants, of which 19,669 are endemic to the country (BFG 2021). Despite this, only 18% area is covered by CUs, which add up to approximately 1.6 million km^2, around 2,300 CUs in Brazil. The area within the CUs is still very small in relation to the size of Brazilian biomes. The Amazon, for example, has only 27.3% territory in protected areas. Other biomes are even less protected, such as the Cerrado 9% and the Caatinga only 7.1% (WWF Unidades de Conservação no Brasil 2019).

The history of the study of galls in CUs begins with Lara & Fernandes (1996) in areas of the Serra do Cipó National Park (Minas Gerais). And subsequently, important contributions were given to the South region (*e.g.*, Flor 2020, Mendonça Jr et al. 2010, Mendonça Jr 2011), Southeast (*e.g.*, Fernandes et al. 2001, Carneiro et al. 2009, Maia et al. 2014, Maia & Mascarenhas 2017), Central-West (*e.g.*, Bergamini et al. 2017, Urso-Guimarães et al. 2021), North (*e.g.*, Almada & Fernandes 2011, Julião et al. 2014), and Northeast (*e.g.*, Santos et al. 2011a, b, Santos et al. 2012). However, due to the size and importance of CUs in the Neotropical region, there is still much to be done, aiming to increase knowledge about the ecology and biology of the organisms involved in the gall-inducing insect-host plant interaction in CUs throughout Brazil.

The Chapada Diamantina National Park (Chapada Diamantina Parna) is an example of the few conservation areas in the state of Bahia (Harley & Simmons 1986, Giulietti et al. 1997, Silva et al. 2004) and the largest legally protected area outside the Amazon (Funch et al. 2009). Despite this, it has never been considered for a study of galls, consequently, the knowledge of the interactions established between inducers of galls and their host plants is completely unknown.

Considering that the Chapada Diamantina Parna is an area of maximum priority in the Brazilian Northeast with high biodiversity and level of endemism (Harley & Simmons 1986, Giulietti et al. 1997, Silva et al. 2004) and that no attention has been given to know its galls and host plants, this study aimed to survey and characterize the galls, providing a list of morphotypes, host plants and gall-inducing insects at the Chapada Diamantina Parna, Lençóis (Bahia), as well as to investigate trends in research on gall-inducing insects in CUs in

Brazil to contribute to future biological and ecological studies in Brazilian CUs.

MATERIALS AND METHODS

Study area

The Chapada Diamantina is in the Espinhaço Mountain Range, in the state of Bahia, covering different ranges, including the Serra do Sincorá (CPRM 1994), which occupies the central part of the eastern edge of Chapada, including the Chapada Diamantina Parna (12°25'–13°20'S and 41°35'41°20'W) (Funch & Harley 2007). In the phytogeographic domain of the Caatinga, the Chapada Diamantina Parna have 1,520 km^2 and is formed by a mosaic of landscapes and vegetation cover. The relief is quite uneven, with large residual massifs, rocky tops, steep slopes and deep narrow valleys, and high, narrow, and elongated mountain ranges (Misi & Silva 1994). Lençóis is one of the six municipalities that comprise Chapada Diamantina Parna (Figura 1) and has all the different vegetation types found in the limits of the park, namely: cerrado *stricto sensu* with discontinuous areas of arboreal elements and continuous areas dominated by herbaceous vegetation and small bushes; rupestrian field with areas comprising herbs, subshrubs, shrubs, and small trees that generally grow at altitudes above 900 m in poor soils and forest formations, ranging from submontane to montane, and from semi-deciduous to deciduous or evergreen (Franca-Rocha et al. 2004, Santos et al. 2021). The climate of the region is Tropical Semi-humid (Alvares et al. 2013), with a marked rainy season (November to March) and a strong dry season (July to November) (Funch et al. 2009). The average annual rainfall is above 1,000 mm and the average annual temperatures range between 18 and 22 ºC (Funch et al. 2009).

Sampling of galls and host plants

Galls and their host plants were collected in areas of cerrado s.s., rupestrian field, secondary montane forest, and gallery forest in the period of

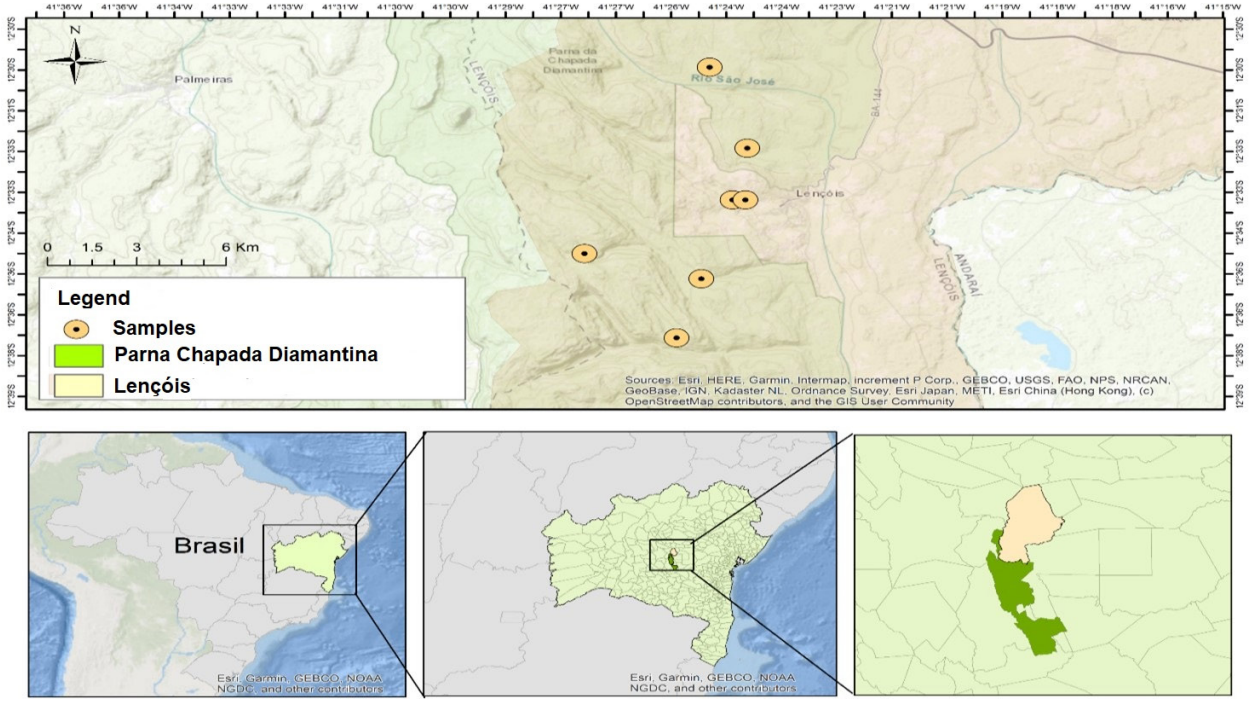

Figure 1. Geographic Location of the Chapada Diamantina National Park, Lençóis, state of Bahia, Brazil.

one year, from August 2021 to July 2022, covering the dry and rainy seasons. Monthly collections were taken in different locations (Table I), namely Bodão Waterfall, Mandassaia River, Poço Harley, Primavera Waterfall, Palmital Waterfall, Ribeirão do Meio, Sossego Waterfall, and Vale do Lapão. The altitude of each collection location and its area were obtained in the field by GPS. Each collection was carried out by two people and lasted eight hours per trip, totaling 96 hours of sampling effort.

All architectures of plants (herbaceous, shrubs, trees, and lianas) up to 2 meters in height were inspected. Information about the external morphology of the galls was recorded in the field, such as organ of occurrence, shape, and color. Regarding the shape of the gall, the terminology proposed by Isaias et al. (2013) was adopted. All galls were photographed in the field to help characterize the morphotypes. Samples of the collected host plants were herborized for identification based on consultation with the specialized literature that provides identification keys, consultation with specialists, and comparison with the collections of the herbarium of the Universidade do Estado da Bahia (HUNEB, Caetité collection). The APG IV classification system (2016) was followed for family circumscriptions. Information on geographic distribution and the spelling of the scientific names of host plants were checked on the Flora e Funga do Brasil website (http://floradobrasil.jbrj.gov.br).

To obtain the gall-inducing insects and associated fauna, samples of each gall morphotype collected were transported in sealed plastic bags and duly identified. In the laboratory, each gall was morphologically characterized and separated into two lots, one for dissection to describe its internal structure and obtain immature insects and the other to obtain adult insects and associated fauna. Each gall was placed separately in plastic pots, sealed, and labeled, with a piece of cotton dampened in water to maintain the humidity of the environment and inspected daily. When there was more than one gall morphotype simultaneously in the same organ (which is common in the case of leaves), morphotypes were separated so that there was no mixing of the fauna associated with different galls. The other part of the samples was dissected with the aid of a stereomicroscope to remove the larvae. At this stage, we recorded the number

Table I. Gall collection sites and host plants occurring in the Chapada Diamantina National Park, in the municipality of Lençóis, state of Bahia, Brazil.

Phytophysiognomy	Locality	Geographic coordinates	Altitude	Length (trail hike round trip)
Cerrado *s.s.*	Bodão Waterfall	12º35'00" S, 41º27'04" W	1,024 m	6 km
Rupestrian field	Palmital Waterfall	12º37'04" S, 41º25'24" W	771 m	6 km
Rupestrian field	Bodão Waterfall	12º35'37" S, 41º24'57" W	430 m	12 km
Cerrado *s.s.*	Primavera Waterfall	12º33'41" S, 41º24'23" W	565 m	6 km
Gallery forest	Poço Harley	12º33'41" S, 41º24'09" W	466 m	4 km
Cerrado *s.s.*	Ribeirão do Meio	12º34'17" S, 41º23'24" W	371 m	7 km
Montane forest	Mandassaia River	12º30'26" S, 41º24'48" W	743 m	6 km
Cerrado *s.s.*	Vale do Lapão	12º32'25" S, 41º24'07" W	587 m	6 km

of internal larval chambers. All insects obtained were preserved in 70% ethanol and sent to the Diptera Laboratory of the Museu Nacional, Universidade Federal do Rio de Janeiro, to be identified.

Studies of galls in Brazilian Conservation Units

Articles on gall-inducing insect surveys in Brazilian CUs were compiled from articles indexed on the platform "Portal de Periódicos Capes" (www.periódicos.capes.gov.br) and Google Scholar (https://scholar.google.com.br) in May 2022, using the keywords "insect", "galls" and "conservation units", the results of the articles had their titles, abstracts and, when necessary, the full text inspected to filter only studies on gall-inducing insects in CUs in Brazil. Thus, articles were included in the compilation only when there was an explicit indication that the study was wholly or partially carried out in conservation units in Brazil.

Statistical analyses

To evaluate the association of the percentage of gall morphotypes and gall inducing orders in relation to vegetation type and host plant families, we used Pearson's chi-square tests and Fisher's exact test. The Yates's correction was applied whenever necessary in chi-square analyses. In case of significant results, pairwise comparisons were performed considering the significance (*p*-value) with Bonferroni correction. All analyses were performed in R 4.3.0 (R Core Team 2023).

RESULTS

Survey of galls

Along the eight studied trails at the Chapada Diamantina Parna, 107 gall morphotypes were recorded in 88 species, belonging to 77 genera and 38 botanical families (Table II, Figures 2-7). Of the total number of morphotypes, most were found in cerrado *s.s.* vegetation (n=71; 67%) followed by areas of montane forest (n=24; 22%), gallery forest (n=7; 7%), and rupestrian fields (n=5; 4%).

Most galls were induced in species of the families Myrtaceae (n=10) and Fabaceae (n=8), followed by Melastomataceae (n=7) and Malpighiaceae (n=7). The genera with the highest gall richness were *Eugenia* L. (Myrtaceae) (n=5), *Copaifera* L. (Fabaceae) (n=4), and *Byrsonima* Rich. ex Kunth (Malpighiaceae) (n=4). All morphotypes found in the Chapada Diamantina Parna are new records for the park. Galls were also recorded for the first time in Brazil on *Paralychnphora bicolor* (DC.) MacLeish (Asteraceae) (Figure 2j), *Handroanthus chrysotrichus* (Mart. ex DC.) Mattos (Bignoniaceae) (Figure 2n), *Periandra coccinea* (Schard.) Benth. (Fabaceae) (Figure 4b), *Senna multijuga* (Rich.) H.S. Irwin & Barneby (Fabaceae) (Figure 4c), *Luehea candicans* Mart. (Malvaceae) (Figure 4r), and *Marcetia bahiensis* (Brade & Markgraf) Wurdack. (Melastomataceae) (Figure 5a). Eight are endemic to Brazil: *Marcetia bahiensis, Paralychnphora bicolor*, *Periandra coccinea, Copaifera duckei* Dwyer (Fabaceae), *Copaifera luetzelburgii* Harms (Fabaceae), *Eugenia catharinae* O. Berg (Myrtaceae), *Manihot tripartite* (Spreng) Müll. Arg., (Euphorbiaceae), and *Qualea cryptantha* (Spreng.) Warm. (Volchysiaceae).

The vast majority of galls were induced on leaves (n=76%), preferentially on the adaxial face (n=58%) followed by the stem (n=20%) and more rarely in buds (n=2%) (Figure 4t), flowers (n=1%) (Figure 4b) and fruit (n=1%) (Figure 2a). All morphotypes occurred in a single plant organ, with only one exception, the globoid galls induced in an unidentified species of Boraginaceae (Figure 5s), observed both on the stem and on the leaves in cerrado *s.s.* areas.

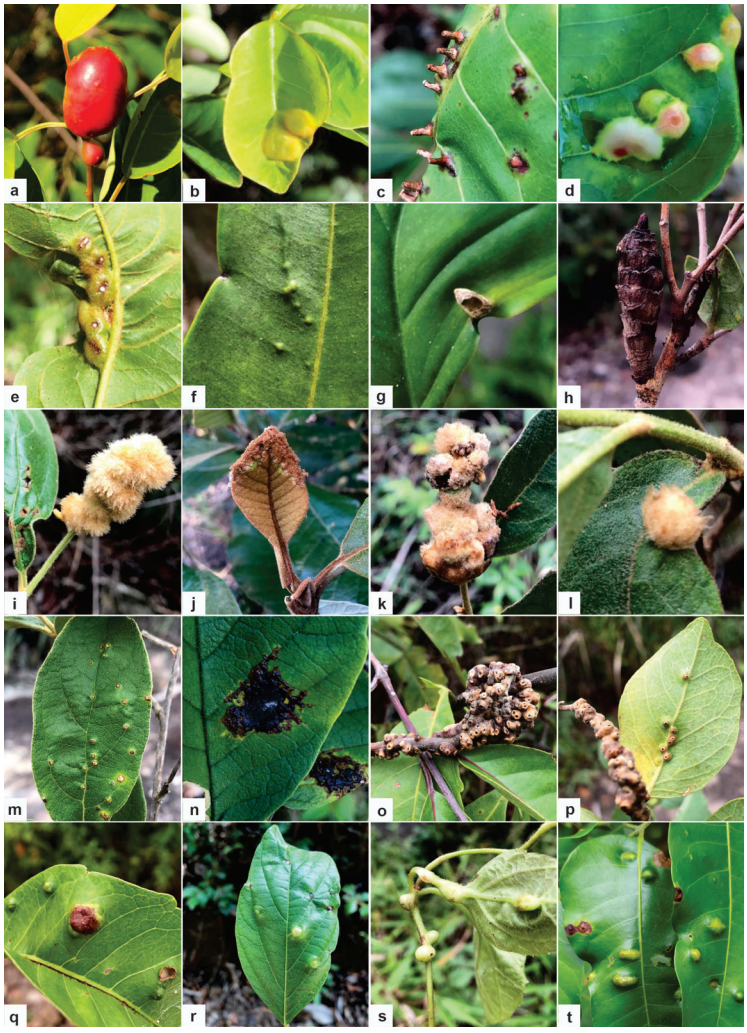

Figure 2. Entomogenous galls at the Chapada Diamantina National Park, Lençóis, state of Bahia, Brazil. a-b. *Astronium fraxinifolium* Schott ex Spreng; c. *Anacardium* sp.; d. Anacardiaceae Indet. e. *Duguetia flagellaris* Huber; f. *Annona* sp.; g. *Thaumatophyllum* sp.; h. *Baccharis minutiflora* Mart. ex Baker; i. *Moquiniastrum paniculatum* (Less) G. Sancho; j. *Paralychnophora bicolor* (DC.) MacLeish; k-l. Asteraceae Indet. 1. m. Asteraceae Indet. 2. n. *Handroanthus chrysotrichus* (Mart. Ex DC.) Mattos; o-p. Bignoniaceae Indet. 1; q. Bignoniaceae Indet. 2; r. Bignoniaceae Indet. 3; s. Boragnaceae Indet.; t. *Protium heptaphyllum* (Aulb.) Marchand. Photos: Gabriela Bomfim.

Galls occurred in plants with different habits: shrubs (n=51%), trees (n=29%), subshrub (n=13%), herbs (n=5%), and lianas (n=2%). They are grouped into six different shapes: globoid (n=44%), lenticular (n=19%), fusiform (n=18%), conical (n=3%), leaf fold (n=2%), and marginal Roll (n=1%). There was also a record of amorphous galls in 13% morphotypes (n=15). Most occurred in groups (n=69%) and had only one larval chamber (n=84%). Among the analyzed morphotypes, 78% did not present trichomes, that is, they were glabrous (Table I).

Concerning color, green (n=41%) (Figure 3i), brown (n=32%) (Figure 3s), white (n=8%) (Figure 4r), yellow (n=7%) (Figure 5j), or, more rarely, purple (n=5%) (Figure 5r), red (n=4%) (Figure 5q), black (n=2%) (Figure 2n), and orange (n =1%) galls were found (Figure 2a). Stem galls induced in an unidentified Fabaceae species (Figure 4d) varied in color, from yellowish at the beginning of their developmental stage to brown when senescent.

Of the 107 gall morphotypes recorded here, the gall-inducing insects of only 22 were identified (14 at the family level and only four at the species level, *Lopesia linearis* Maia, 2003, *Lopesia similis* Maia, 2004, *Myrciaryiamia admirabilis* Maia, 2007, and *Schismatodiplosis lantanae* Rübsaamen, 1916 (Diptera, Cecidomyiidae). Among the gall-inducing insects not identified at the species level are representatives of the order Diptera

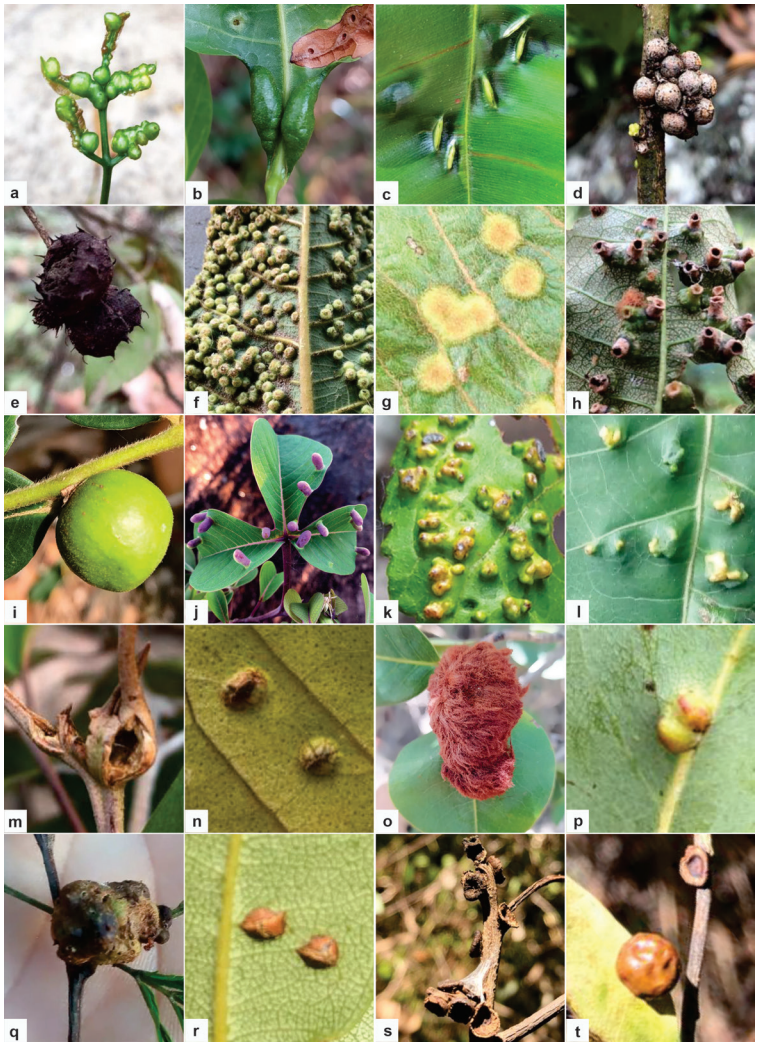

Figure 3. Entomogenous galls at the Chapada Diamantina National Park, Lençóis, state of Bahia, Brazil. a-b. *Protium heptaphyllum* (Aulb.) Marchand; c. *Calophyllum brasiliense* Cambess.; d. *Calophyllum* sp. e. Clusiaceae Indet.; f. *Combretum Glaucocarpum* Mart.; g. *Terminalia* sp.; h. *Parinari obtusifolia* Hook. f.; i. *Diospyros* sp.; j. *Manihot tripartite* (Spreng) Müll. Arg.; k-l. *Croton* sp.; m-n. Euphorbiaceae indet.; o. *Erythroxylum suberosum* A. St. – Hil.; p. *Erythroxylum* sp.; q. *Calliandra dysantha* Benth.; r. *Copaifera duckei* Dwyer; s-t. *Copaifera langsdorffii* Desf. Photos: Gabriela Bomfim.

(Cecidomyiidae) (n=13), Hymenoptera (n=3), Coleoptera (n=1), and Lepidoptera (n=1) (Table II). Regarding the associated fauna, parasitoids Hymenoptera (n=15), inquilines, Thysanoptera (n=3), Lepidoptera (n=2), and Coleoptera (n=1), and successors, Formicidae (n=3), Psocoptera (n=1), and mites (n=1) were recorded (Table II).

The results indicated that the percentage of gall inducing orders were not associated to vegetation type (χ^2 = 14.7, df = 9, p = 0.098) and host plant family (Fisher's exact test: p = 0.367). However, the percentage of gall morphotypes were associated to vegetation (χ^2 = 90.9, df = 3, p < 0.001), indicating that cerrado and montane forest harboured more gall species compared to other phytophysiognomies (p < 0.004 in all cases) (Figure 8a). Host plant species was also associated to the percentage of gall species (χ^2 = 63.0, df = 37, p = 0.005), but pairwise comparisons were not significant in any case (Figure 8b).

Studies of galls in Brazilian Conservation Units

A total of 46 gall surveys carried out in Brazilian CUs were published from 1996 to 2022 (Table III, Figures 9-10). The number of publications found has increased over the years, especially in the last decade. The vast majority of gall surveys were carried out in the Southeast region of Brazil (n=27 studies) (Table III). The Central-West, North, South, and Northeast regions were less studied, with four, four, six and six studies,

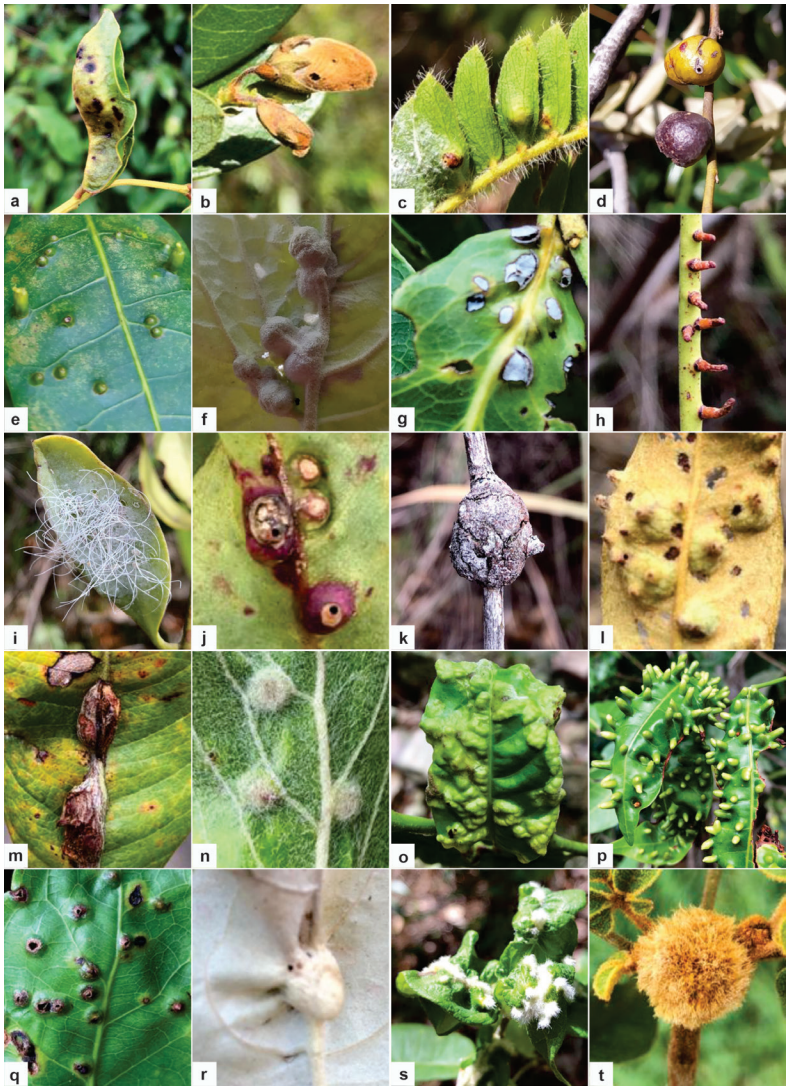

Figure 4. Entomogenous galls at the Chapada Diamantina National Park, Lençóis, state of Bahia, Brazil. a. *Copaifera luetzelburgii* Harms; b. *Periandra coccinea* (Schard.) Benth.; c. *Senna multijuga* (Rich.) H.S. Irwin & Barneby; d. Fabaceae Indet.; e. Lauraceae Indet. 2.; f. Lauraceae Indet. 2; g. Lauraceae Indet. 3; h-i. *Struthanthus* sp.; j. Lythraceae Indet.; k-m. *Byrsonima gardneriana* A. Juss.; n. *Byrsonima guilleminiana* A. Juss.; o. Malpighiaceae Indet. 1; p. Malpighiaceae Indet. 2; q. Malpighiaceae Indet. 3; r. *Luehea candicans* Mart.; s. *Helicteres* sp.; t. *Macairea radula* (Bonpl.) DC. Photos: Gabriela Bomfim.

respectively (Figures 8-9). Among the Brazilian states, Minas Gerais led in the number of papers (n=13), followed by Rio de Janeiro (n=10) and Pernambuco (n=4) (Table III).

DISCUSSION

Approximately 27 years ago, Brazilian researchers began studying galls in CUs in Brazil, the first work was carried out by Lara & Fernandes (1996) in the Serra do Cipó National Park in Minas Gerais, but the host plants were not scientifically identified. Since then, the number of gall surveys in CUs has been increasing in different regions of Brazil, with the majority carried out in the Southeast region. The present study documents an increasing trend in the scientific production on gall-inducing insects in CUs, but it reflects a geographic bias: the researchers involved are concentrated in the southeastern region of Brazil, mainly in the states of Minas Gerais and Rio de Janeiro.

Of the 26 Brazilian states, there are surveys of galls in 12 of them, with the states of Minas Gerais and Rio de Janeiro with the highest number. Only one published study was conducted in a CU in the state of Bahia, our study is the second; this can be because surveys of galls in this state

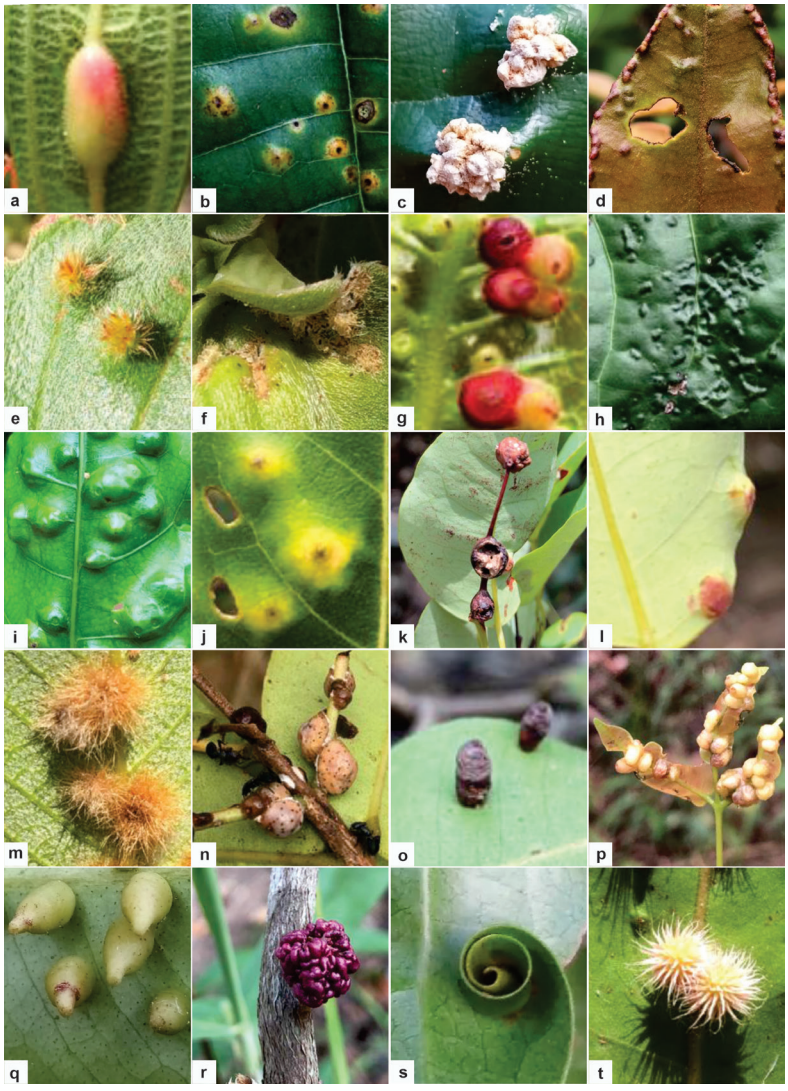

Figure 5. Entomogenous galls at the Chapada Diamantina National Park, Lençóis, state of Bahia, Brazil. a. *Marcetia bahiensis* (Brade & Markgraf) Wurdack.; b. *Miconia albicans* (SW.) Triana; c. *Miconia alborufescens* Naudin; d. *Miconia* sp. e. *Leandra* sp.; f. *Tibouchina* sp.; g. *Trichilia catigua* A. Juss.; h-i. *Guarea* sp.; j. Meliaceae Indet.; k-l. *Eugenia catharinae* O. Berg; m- *Campomanesia* sp. n-p. *Eugenia* sp.; q. *Myrcia neoobscura* E.Lucas & C.E.Wilson; r. Myrtaceae Indet. 1; s. Myrtaceae Indet. 2; t. Myrtaceae Indet. 3. Photos: Gabriela Bomfim.

are recent and still punctual (Costa et al. 2014a, b, Nogueira et al. 2016, Brito et al. 2018, Lima & Calado et al. 2018, Vieira et al. 2018, Santana et al. 2020, Campos et al. 2021, Santos-Silva et al. 2022, Melo & Santos-Silva 2023), which reinforces the need for greater collection effort, especially in neglected CUs to minimize sampling bias and provide a better knowledge base of the richness of gall-inducing insects and their host plants for the conservation of these organisms.

In the present study, the number of morphotypes found, 107 galls induced in 88 host plant species, is considered relatively high compared to other surveys carried out in CUs in Brazil (Table III). For example, in Serra Verde State Park (MG), 75 gall morphotypes were recorded in 43 plant species during twelve monthly collections in the Cerrado (Santana & Isaias et al. 2014), while in Praia do Sul State Biological Reserve (RJ), 36 morphotypes were observed in 22 host species that grow in restinga areas surveyed in two monthly collections (Maia & Oliveira 2010), and at the Serra dos Pireneus State Park (GO), 21 different types of galls were surveyed in 21 species of host plants in different Cerrado phytophysiognomies during twelve collections in quarterly trips (Araújo et al. 2007). Even considering differences in sampling

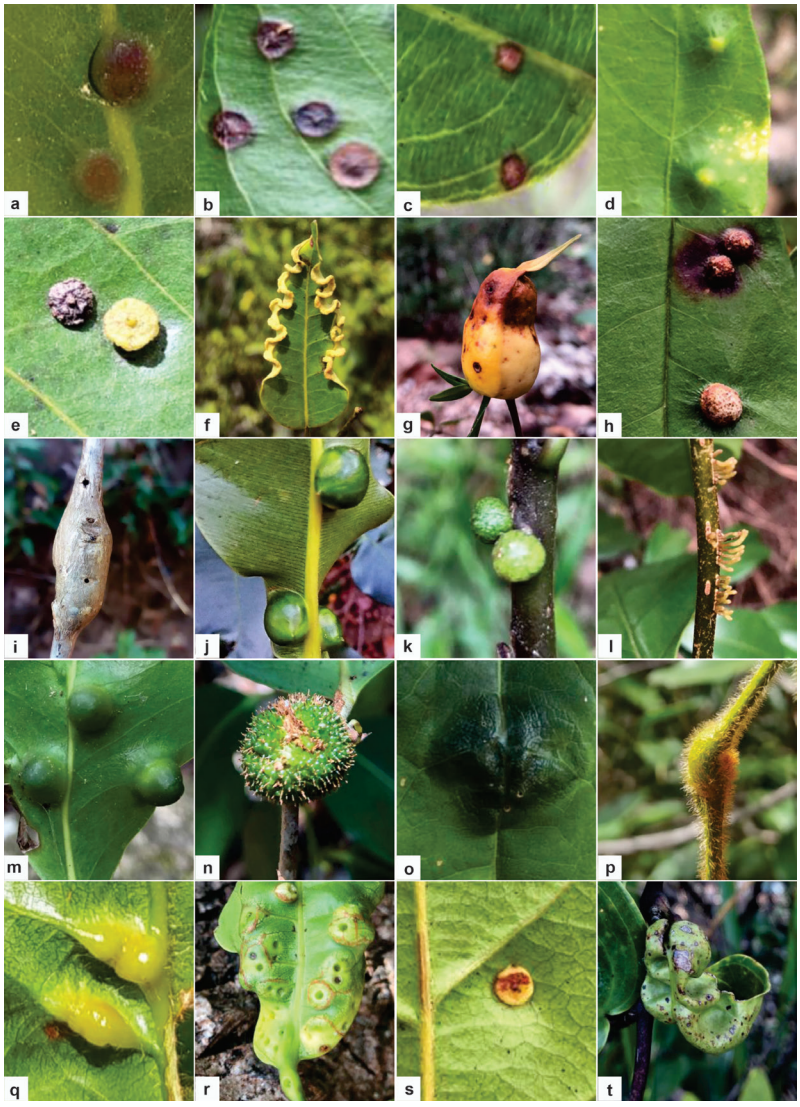

Figure 6. Entomogenous galls at the Chapada Diamantina National Park, Lençóis, state of Bahia, Brazil. a. Nyctaginaceae Indet.; b. *Ouratea nana* (A. St. Hil.) Engl. c. *Ouratea* sp.; d. *Passiflora* sp.; e. *Pogonophora schomburgkiana* Miers ex Benth.; f. Phyllanthaceae Indet.; g. *Piper arboretum* Aubl.; h. Proteaceae Indet.; i-j. *Randia armata* var. *pubescens* (K. Schum.) Standl.; k. *Psychotria* sp.; l. Rubiaceae Indet. 1; m. Rubiaceae Indet. 2; n. *Allophylus racemosus* Sw.; o. *Serjania glabrata* Kunth. p-q. Sapindaceae Indet.; r. *Pouteria torta* (Mart.) Radlk.; s. *Siparuna guianensis* Aubl; t. *Smilax* sp. Photos: Gabriela Bomfim.

effort, the richness of host plants, and other variables, our data reveal the potential of the Chapada Diamantina Parna for the conservation of gall-inducing insects and their host plants. In addition, the record of six new morphotypes in six different plant species for Brazil further reinforces the importance of this unit for the conservation of gall-inducing insects and corroborates studies that predict that the richness of gall-inducing insects is high and poorly studied in CUs in Brazil (Santana & Isaias 2014).

At the Chapada Diamantina Parna, the phytophysiognomy of the cerrado s.s. gathers most of the galls (n=67%), compared to the other investigated phytophysiognomies, corroborating other studies that indicate that the Cerrado biome and its phytophysiognomies have the richest fauna of gall-inducing insects in Brazil (Araújo 2018, Cintra et al. 2020, Campos et al 2021). This biome is confirmed as home to the richest savanna flora in the world (Forzza et al. 2012) and hosts a greater number of galls, with a record of approximately 968 interactions between gall-inducing insects in 505 host plants (Cintra et al. 2020).

At the Chapada Diamantina Parna, family Myrtaceae together with Fabaceae hosted the

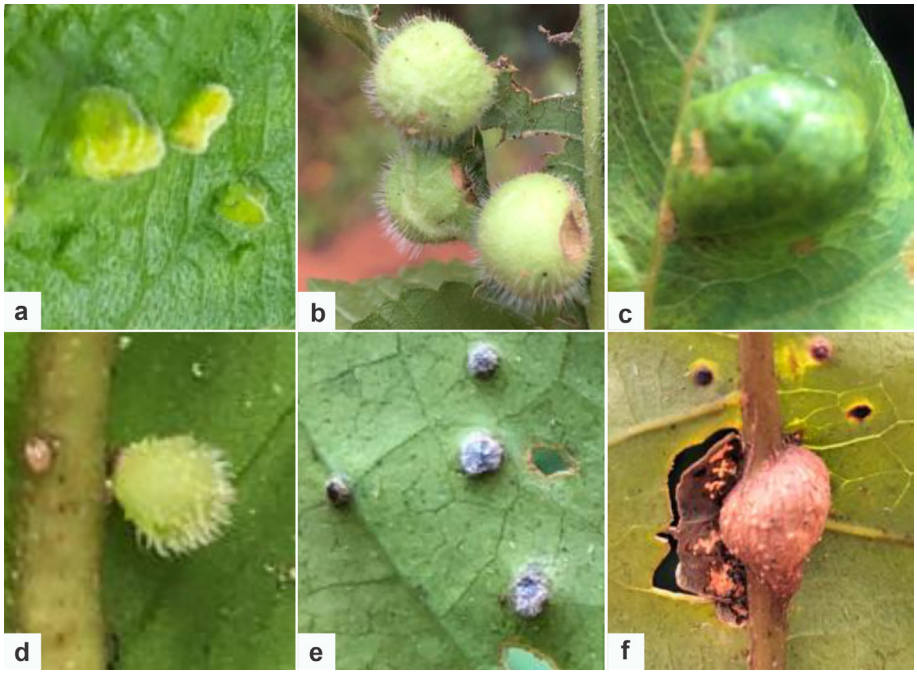

Figure 7. Entomogenous galls at the Chapada Diamantina National Park, Lençóis, state of Bahia, Brazil. a-b. *Lantana camara* L; c. *Qualea cryptantha* (Spreng.) Warm. d. *Qualea parviflora* Mart.; e-f. *Drimys brasiliensis* Miers. Photos: Gabriela Bomfim.

highest number of galls, which reflects the diversity of these plant families in the local flora. Santos et al. (2021) recorded 82 species and 9 genera of Myrtaceae in the limits of the Chapada Diamantina Parna and its surroundings, especially in the municipality of Lençóis. A similar result is observed for the Fabaceae family, which leads in different floristic surveys and phytophysiognomies at the Chapada Diamantina Parna as well as in the seasonal forest (Couto et al. 2011), in the cerrado (Grillo 2008), and in the gallery forest (Ribeiro-Filho et al. 2009). The main reason for the great importance these families as a super-host of galls is the relatively large number of Brazilian species. According to the plant taxon size hypothesis, species-rich families tend to host a higher richness of gall-inducing insects (Fleck & Fonseca 2007).

The genera *Eugenia*, *Copaifera,* and *Byrsonima* had the highest gall richness in the studied phytophysiognomies of the Chapada Diamantina Parna, here considered super-hosts, as has already been registered for cerrado and rupestrian field environments in Bahia (Costa et al. 2014a, Nogueira et al. 2016, Campos et al. 2021, Vieira et al. 2018), and the caatinga-cerrado transition in northern Minas Gerais (Luz et al. 2012). These same genera were observed to be richer in species at the Chapada Diamantina Parna, *Eugenia* (Santos et al. 2021), *Copaifera,* and *Byrsonima* (Couto et al. 2011), which corroborates the hypothesis of floristic diversity, taxa with greater richness are also the most abundant in the occurrence of galls (Fernandes & Price 1988, Veldtman & Mcgeoch 2003, Espírito-Santo & Fernandes 2007).

Most galls were found on shrubs (n=51%) and trees (n=29%), and were significantly rare on herbs (n=5%), and lianas (n=2%). This is a common pattern in different surveys carried out in Brazil (Cuevas-Reyes et al. 2004, Araújo et al. 2006, Espírito-Santo & Fernandes 2007, Gonçalves-Alvim & Fernandes 2001, Lara et al. 2002). This can be explained by the plant architecture hypothesis that the greater the architectural complexity of the plant, the greater the richness and abundance of associated herbivore insects (Lawton & Schröder 1977, Lawton 1983).

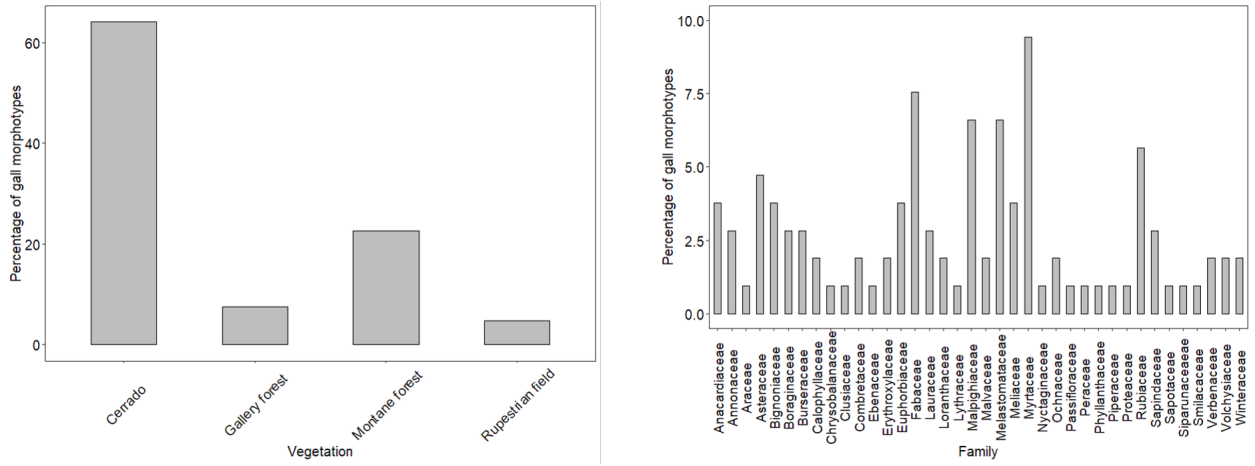

Figure 8. Bar charts indicating chi-square significant results for the association between percentage of gall morphotypes and (a) vegetation type and (b) host plant family. For vegetation type, pairwise comparisons indicated that cerrado had more gall species than other phytophysiognomies, and montane forest in relation to gallery forest and rupestrian field. No significant results were found in pairwise comparisons among host plant families.

Almost all galls occurred in only one plant organ, with a single exception of the induced gall on an unidentified species of the Bignoniaceae family, whose galls occur on both stems and leaves, confirming the specificity of the gall-inducing insect for the host plant organ (Dreger-Jauffret & Shorthouse 1992). The highest number of induced galls on leaves (n=76%) followed by stems (n=20%), as observed in this study, is similar to the patterns recorded for Brazil (*e.g.*, Fernandes & Negreiros 2006, Santos et al. 2011a, b, 2012, Toma & Mendonça Jr 2013, Santana & Isaias 2014, Nogueira et al. 2016, Silva et al. 2018), including its different conservation units (*e.g.*, Gonçalves-Alvim & Fernandes 2001, Araújo et al. 2007, Bregonci et al. 2010, Santana & Isaias 2014). This is because leaves are considered more plastic host organs compared to stems (Isaias et al. 2013). Moreover, they are generally the most available and abundant plant organs, being easily observed, in contrast to the others (Santana & Isaias 2014). Leaves also have higher levels of nutritional reserves due to their photosynthetic capacity (Castro et al. 2012). Considering the occurrence of galls on available leaf surfaces, 42% registered morphotypes were induced on the abaxial face. Edward & Wratten (1998) point out that the abaxial face offers less stressful microclimatic conditions than the adaxial surface.

The induction of galls on buds, fruits, and flowers is less frequent in surveys throughout Brazil. At the Chapada Diamantina Parna, it is not different, only two globoid galls were induced in buds of *Macairea radula* (Bonpl.) DC. (Melastomataceae) and an unidentified species of the Euphorbiaceae family, both occurring in the cerrado *s.s.* Galls on buds were also recorded by Maia & Oliveira (2010) in Praia do Sul State Biological Reserve in *Erythroxylum ovalifolium* Peyr. (Erythroxylaceae), *Dalechampia leandrii* Baill. (Euphorbiaceae), *Myrciaria jaboticaba* (Vell.) O. Berg (Myrtaceae), and *Psidium cattleianum* Sabine (Myrtaceae). In the reproductive structures, a fusiform gall was found in the fruit of *Astronium fraxinifolium* Schott ex Spreng (Anacardiaceae). In Brazil, there is a record of galls on the fruit of *Fridericia conjugata* (Vell.) Mart. (Bignoniaceae) (Maia & Silva 2016) and *Davilla rugosa* Poir. (Dilleniaceae)

Table III. Surveys of galls and their host plants in Conservation Units in Brazil.

Region	State	Conservation Unit (Author)	Morphotypes of galls and host plants
South	Rio Grande do Sul	Itapeva State Park (Mendonça Jr et al. 2010)	104 morphotypes, 75 species
		Espinilho State Park (Mendonça Jr 2011)	59 morphotypes, 23 species.
		Pró-Mata Center for Research and Nature Consevation (Toma & Mendonça Jr 2013).	57 morphotypes, 43 species.
	Santa Catarina	Acaraí State Park	15 morphotypes, 8 species (Arriola et al. 2015). 56 morphotypes, 31 species (Arriola & Melo Jr 2016)
		Maracajá Ecological Park (Flor 2020)	3 morphotypes, 2 species.
Southeast	Espirito Santo	Paulo State Park César Vinha (Bregonci et al. 2010).	38 morphotypes, 21 species.
		Santa Lúcia Biological Station, Augusto Ruschi Biological Reserve, São Lourenço Municipal Natural Park (Maia et al. 2014)	265 morphotypes, 141 species
	Minas Gerais	Serra do Cipó National Park (Lara & Fernandes 1996).	Gall-inducing insects (46 species in a census of 45 trees, 100 shrubs, and 1,000 herbs per site).
		Pirapitinga Ecological Station (Gonçalves-Alvim & Fernandes 2001).	92 morphotypes, 62 species.
		Caraça National Park, Rio Doce State Park (Fernandes et al. 2001).	177 morphotypes, 94 species.
		Serra de São José Environmental Protection Area (Maia & Fernandes 2004).	137 morphotypes, 73 species.
		Bulcão Farm Private Natural Heritage Reserve (Fernandes & Negreiros 2006).	29 morphotypes, 24 species.
		Itacolomi State Park, Serra de Ouro Branco State Park, Serra do Caraça Private Natural Heritage Reserve, Rio Preto State Park, Grão Mogol State Park, Biribiri State Park (Carneiro et al. 2009).	241 morphotypes, 141 species.
		Serra do Cipó National Park (Coelho et al. 2009).	92 morphotypes, 51 species.
		Pandeiros River Environmental Protection Area (Luz et al. 2012).	98 morphotypes, 70 species.
		Unilavras-Boqueirão Biological Reserve (Malves & Frieiro-Costa 2012).	57 morphotypes, 43 species.
		Brigadeiro State Park, Caparaó National Park, Ibitipoca State Park (Coelho et al. 2013).	73 morphotypes, 30 species.
		Serra Verde State Park (Santana & Isaias 2014).	75 morphotypes, 43 species.

Table III. Continuation.

		Serra do Brigadeiro State Park, Caparaó National Park, Ibitipoca State Park (Coelho et al. 2013).	38 morphotypes, 22 species. 23 morphotypes, 21 species. 21 galhas, 13 species.
		Serra Negra do Funil Natural Heritage Private Reserve (Maia & Mascarenhas 2022)	63 gall morphotypes, 48 plant species.
	Rio de Janeiro	Maricá Environmental Protection Area (Maia 2001)	108 morphotypes, 53 species.
		Restinga de Jurubatiba National Park (Monteiro et al. 2004)	99 morphotypes, 40 species.
		Grumari Environmental Protection Area and Grumari Municipal Natural Park (Oliveira & Maia 2005)	43 morphotypes, 25 species
		Praia do Sul State Biological Reserve (Maia & Oliveira 2010)	36 morphoyupes, 22 species
		Itatiaia National Park (Coelho et al. 2013)	20 morphotypes, 20 species.
		Guaxindiba State Ecological Station (Maia & Carvalho-Fernandes et al. 2016).	143 morphotypes, 82 species.
		Costa do Sol State Park, Caruara Private Natural Heritage Reserve (Carvalho-Fernandes et al. 2016).	151 morphotypes, 82 species.
		Itatiaia National Park (Maia & Mascarenhas 2017)	143 morphotypes, 24 families
		União Biological Reserve (Maia & Souza 2020)	153 morphotypes, 55 families.
		Boca da Barra Municipal Park (Rodrigues & Maia 2020)	8 morphotypes, 5 species.
	São Paulo	Pé-de-Gigante Reserve (Urso-Guimarães & Scareli-Santos 2006)	36 morphotypes, 25 species.
		Jataí Ecological Station (Saito & Urso-Guimarães 2012).	69 morphotypes, 41 species.
Central-West	Goiás	Emas Nacional Park Serra dos Pireneus State Park	97 morphotypes, 55 species (Araújo et al. 2014) 21 morphotypes, 21 species (Araújo et al. 2007). 68 morphotypes, 51 species (Araújo et al. 2011).
	Mato Grosso	Chapada dos Guimarães National Park (Urso- Guimarães et al. 2021).	295 morphotypes, 140 species.
North	Amazonas	Reserve of the Biological Dynamics of Forest Fragments Project.	886 morphotypes, 359 species (Julião et al. 2014). 27, morphotypes, 27 morphospecies (Silva et al. 2011).
	Pará	Saracá Taquera National Park	309 morphotypes, 255 species (Almada & Fernandes 2011). 112 morphotypes, 65 species (Araújo et al. 2012).

Table III. Continuation.

Northeast	Bahia	Chapada Diamantina National Park, Municipality of Lençóis (Present study).	107 morphotypes, 88 species.
		Raso da Catarina Ecological Station (Santos-Silva et al. 2022).	16 morphotypes, 5 species.
	Pernambuco	Vale do Catimbau National Park (Municipality of Buíque) (Santos et al. 2011a).	33 morphotypes.
		Bonito Municipal Reserve, Serra Negra Biological Reserve, João Vasconcelos Sobrinho Municipal Park (Santos et al. 2011b).	80 morphotypes, 49 species.
		Saltinho Ecological Reserve, Dois Irmãos State Park, Carnijó Ecological Reserve, Carnijó Private Natural Heritage Reserve, Mata de Duas Lagoas Ecological Reserve, Charles Darwin Ecological Refuge (Santos et al. 2012).	133 morphotypes, 76 species.
		Dois Irmãos State Park (Carvalho-Fernandes et al. 2009).	32 morphotypes, 9 species.

(Vieira et al. 2018) in Atlantic Forest and Cerrado environments, respectively, for example. Fruits affected by gall-inducing insects may or may not present externally evident deformation, and the galls consist of sets of larval chambers surrounded by lignified tissue that may or may not be fused and/or to seeds. Due to the rigidity of the mature gall and the "cluster of chambers" aspect, it is not possible to define the exact shape or size. This can lead to the misinterpretation that they are just seeds that are all fused (Wikler 1999, 2000).

The predominance of globoid galls resembles the pattern observed in the Neotropical region (Isaias et al. 2013), where it was recorded in caatinga (Santos et al. 2011a, b, Carvalho-Fernandes et al. 2012), cerrado *s.s.* (Nogueira et al. al. 2016, Lima & Calado 2018, Vieira et al. 2018) environments, and in the Atlantic Forest (Carvalho-Fernandes et al. 2009, Alcântara et al. 2017). In conversation units, this same pattern is observed (Araújo et al. 2007, Bregonci et al. 2010, Santana & Isaias 2014).

Most of the recorded galls are green in color, indicating the presence of chlorophyll and the existence of photosynthetic processes, which can be an advantage for host plants, as they increase photosynthetic capacity due to hyperplasia and hypertrophy of plant cells (Magalhães 2010). Green galls can be good models for studying photosynthesis and cytological responses to galling stress, as investigated by Oliveira et al. (2011). Some studies in tropical areas have shown that photosynthesis in galls is not enough to maintain their structure and they are used as accessories to the host plant machinery (Oliveira et al. 2011, Castro et al. 2012). Change in gall color was verified in induced stem gall in an unidentified species of the family Fabaceae. Although these changes are not well understood, they are probably associated with the growth of gall-inducing insects, the development phase of the gall, or even the action of other trophic levels (Dias et al. 2013, Santana & Isaias 2014).

Many gall surveys carried out in Brazil show isolated galls and galls with a single larval chamber as predominant (*e.g.*, Carvalho-Fernandes et al. 2012, Maia & Silva 2016, Alcântara et al. 2017, Vieira et al. 2018, Campos et al. 2021, Urso-Guimarães et al. 2021). Nevertheless, the

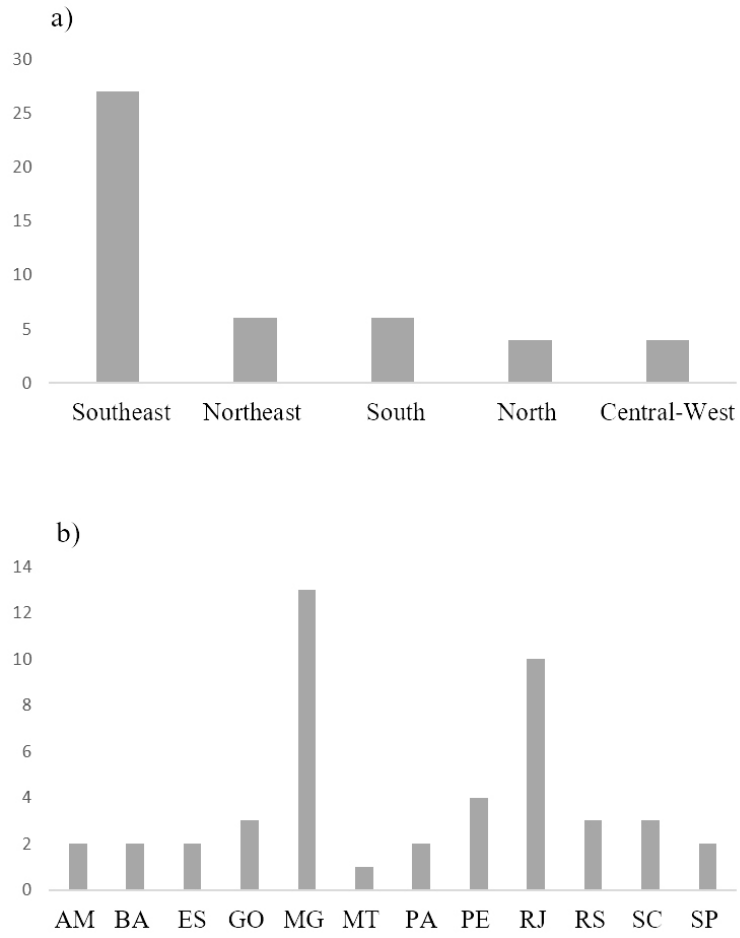

Figure 9. Number of inventories of insect galls carried out in conservation units in Brazil: (a) number of publications for Brazilian regions; and (b) number of publications for Brazilian states.

present study observed a greater number of grouped galls. The distribution of isolated or grouped galls reflects the oviposition pattern of females of each species (Gagné 1994). According to Urso-Guimarães & Scareli-Santos (2006), the occurrence in clusters may be important for the protection of galls by diluting the effects of natural enemies, but further studies are required to prove or disprove these observations.

Glabrous galls, that is, without trichomes, are commonly observed in several surveys carried out in Brazil (Araújo et al. 2007, Costa et al. 2014b, Santana & Isaias 2014, Santana et al. 2020) being frequent in the Brazilian semi-arid region (Nogueira et al. 2016, Vieira et al. 2018, Campos et al. 2021). Trichomes, when present on galls, can provide an adequate microclimate for insect development (Westphal 1992, Boczek & Griffiths 1994), protecting it against high temperatures and water stress.

Gall-inducing insects belong to the orders Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, and Thysanoptera (Maia 2013). Four orders of gall-inducing insects were identified in the phytophysiognomies investigated here, Coleoptera, Diptera, Hymenoptera, and Lepidoptera. Cecidomyiidae (Diptera) were the main inducers of galls, as expected. This family stands out as the group with the highest number of gall-inducing insects in the entire Neotropical region (e.g., Carneiro et al. 2009, Santos et al. 2011a, 2012, Maia 2013, Costa et al. 2014b, Nogueira et al. 2016, Gagné & Jaschhof 2017, Silva et al. 2018, Santana et al. 2020, Santos-Silva & Araújo 2020, Campos et al. 2021)

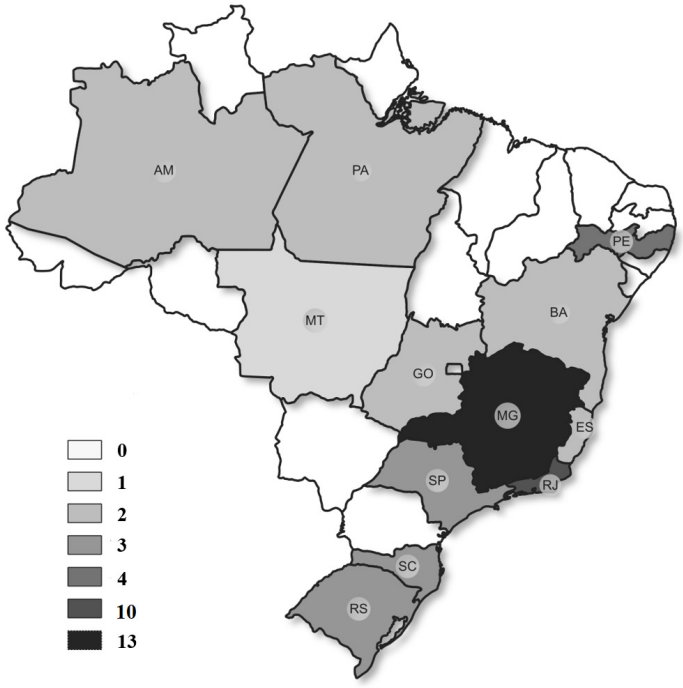

Figure 10. **Geographic distribution of insect gall inventories carried out in conservation units in Brazil.**

and also in conservation units (Maia & Oliveira 2010, Santana & Isaias 2014, Bregonci et al. 2010).

Of the 107 gall morphotypes registered in the present study, inducing insects were identified in only 19, no galls were induced by Hemiptera and Thysanoptera were registered, even though these have been registered in other CUs, such as the Serra Verde State Park (Santana & Isaias 2014) and in the Praia do Sul State Biological Reserve (Maia & Oliveira 2010). This may be related to the difficulty in obtaining specimens of gall-inducing insects (including immatures and adults of both sexes, necessary for species determination), the prevalence of galls that have already been abandoned by their inducer, the lack of knowledge of the biology of inducers; and the lack of taxonomists for known gall-inducing insect groups (Espírito-Santo & Fernandes 2007, Carneiro et al. 2009, Melo Jr 2018). Thus, gall-inducing insects are taxonomically little known, especially in the Neotropics, where most species are new to science (Santana & Isaias 2014). Despite efforts to survey galls in several Brazilian ecosystems, the lack of determination of gall-inducing species is the main gap to be filled, since many studies describe the gall without identifying the gall-inducing agent (Melo Jr et al. 2018).

As indicated in the studies by Maia (2001), other organisms besides the inducers can be found inside the galls, acting as tenants, predators, successors, and parasitoids, these are part of the associated fauna. The gall-associated arthropod fauna at the Chapada Diamantina Parna included Hymenoptera (parasitoids), Coleoptera, Lepidoptera, Thysanoptera, Diptera (cecidophages), Psocoptera, mites and Formicidae (successors). Hymenoptera were identified as the most frequent natural enemies of gall-inducing insects, commonly acting as parasitoids, their habits were verified in the present study, corroborating other surveys throughout Brazil (Maia 2001, Maia & Fernandes 2004). The community of parasitoids (Hymenoptera) associated with host plants in conservation units have been widely reported

in other surveys (Bregonci et al. 2010, Maia & Oliveira 2010, Santana & Isaias 2014). Predatory ants (Hymenoptera: Formicidae) were also found at the Chapada Diamantina Parna associated with three morphotypes of galls. Representatives of Formicidae were also recorded in Serra Geral in Caetité (BA) (Nogueira et al. 2016) and at the Paulo Cesar Vinha State Park (ES) (Bregonci et al. 2010).

As for the successors, mites and Psocoptera, they were less frequent occurring in only one gall morphotype induced in *Byrsonima gardneriana* A. Juss. (Malpighiaceae) and *Copaifera langsdorffii* Desf. (Fabaceae), respectively. In the literature, there are records of representatives of these organisms as successors of galls at the Paulo Cesar Vinha State Park (Bregonci et al. 2010), in species of *Guapira pernambucensis* (Casar.) Lundell (Nyctaginaceae) and *Chaetocarpus myrsinites* Baill. (Peraceae), for example.

The present study documents the increase in gall-inducing insect surveys in Brazilian CUs, with most surveys carried out in the Southeast region, which concentrates the largest number of specialists, demonstrating a geographic bias in the data. This spatial bias associated with the significant number of galls and host plants in the CUs reinforces that there is still much to be done in relation to the study of galls and their host plants in Brazilian CUs. At the Chapada Diamantina Parna, there is a high richness of galls compared to other surveys carried out, with some morphotypes and host species recorded for the first time for Brazil, which evidences the importance of this CU in the conservation of galling insects. Our results also corroborate studies that indicate leaves as the main host organs, the predominance of globoid galls, and the Cecidomyiidae as the main gall inducers.

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SUPPLEMENTARY MATERIAL

Table SI.

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