

A compilation of host plants and their gall-inducing insects for the Caatinga Biome

Fernanda C. F. Cintra¹, Valéria C. Maia², Maria V. Urso-Guimarães³, Walter S. de Araújo⁴,
Marco A. A. Carneiro⁵, Henrique Venâncio⁴, Wanessa R. de Almeida⁶ & Jean C. Santos^{6*}

¹Universidade de São Paulo, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Programa de Pós-Graduação em Entomologia, Ribeirão Preto, SP, Brasil.

²Universidade Federal do Rio de Janeiro, Museu Nacional, Rio de Janeiro, RJ, Brasil.

³Universidade Federal de São Carlos, Departamento de Biologia, São Carlos, SP, Brasil.

⁴Universidade Estadual de Montes Claros, Departamento de Biologia Geral, Montes Claros, MG, Brasil.

⁵Universidade Federal de Ouro Preto, Instituto de Ciências Exatas e Biológicas, Ouro Preto, MG, Brasil.

⁶Universidade Federal de Sergipe, Departamento de Ecologia, São Cristóvão, SE, Brasil.

*Corresponding author: jcsantosbio@gmail.com

CINTRA, F.C.F., MAIA, V.C., URSO-GUIMARÃES, M.V., ARAÚJO, W.S., CARNEIRO, M.A.A., VENÂNCIO, H., ALMEIDA, W.R., SANTOS, J.C. **A compilation of host plants and their gall-inducing insects for the Caatinga Biome.** *Biota Neotropica* 21(4): e20211215. <https://doi.org/10.1590/1676-0611-BN-2021-1215>

Abstract: Caatinga is a seasonally dry tropical forest, one of the richest in plant species. Unfortunately, many groups of herbivorous insects associated with these plants are poorly known. This study aimed to investigate the diversity of gall-inducing insects (GII) and host plants (HP) in the Caatinga. For this, we compiled the information available in the literature of inventories on GII and their HP communities, and the described gall midge species. We found 100 species, 72 genera, and 32 families of HP hosting a total of 156 morphospecies of GII and 12 species of described cecidomyiids. Plant species with only one GII species represented 74% of hosts, but in super HP (i.e., HP with a high number of GII), despite the small number of HP species, there were many GII species. Fabaceae was also the most specious family, with 30% of HP species and 40% of GII. Furthermore, our results showed a low number of species of HP and GII for the Brazilian Caatinga, that we discussed this pattern with the following arguments, first, it is likely that the number of galling insect inventories for the Caatinga is under-sampled, second the Caatinga has a relatively smaller number of plant species when compared to other biomes, and finally, we argue that the Caatinga is a seasonally dry tropical forest where the deciduousness represents a relevant factor in the colonization and performance rates of GII.

Keywords: Galls; Insect gall; Insect herbivores; Seasonally Dry Tropical Forest.

Uma compilação de plantas hospedeiras e seus insetos galhadores para o bioma Caatinga

Resumo: A Caatinga é uma floresta tropical sazonalmente seca, uma das mais ricas em espécies vegetais. Infelizmente, muitos grupos de insetos herbívoros associados a essas plantas são pouco conhecidos. Este estudo teve como objetivo investigar a diversidade de insetos galhadores (IG) e plantas hospedeiras (PH) na Caatinga. Para isso, nós compilamos as informações disponíveis na literatura de inventários sobre a comunidade de IG e suas PH, e as espécies descritas de cecidomídeos. Nós encontramos 100 espécies, 72 gêneros e 32 famílias de PH abrigando um total de 156 morfoespécies de IG e 12 espécies descritas de cecidomídeos. Espécies de plantas com apenas uma espécie de IG representaram 74% das hospedeiras, mas para as super PH (ou seja, PH com alto número de IG), apesar do pequeno número de espécies de PH, havia muitas espécies de IG. Fabaceae foi a família mais rica, com 30% das espécies de PH e 40% dos IG. Além disso, nossos resultados mostraram um baixo número de espécies de PH e IG para a Caatinga brasileira, e discutimos esse padrão com os seguintes argumentos, primeiro, é provável que o número de inventários de insetos galhadores para a Caatinga seja subamostrado, segundo a Caatinga possui um número relativamente menor de espécies vegetais quando comparada a outros biomas e, por fim, argumentamos que a Caatinga é uma floresta tropical sazonalmente seca onde a deciduidade representa um fator relevante para as taxas de colonização e desempenho dos IG.

Palavras-chave: Galhas; Galha de inseto; Insetos herbívoros; Floresta Tropical Sazonalmente Seca.

Introduction

The Neotropical Seasonally Dry Forests are found from Northwestern Mexico to Northern Argentina and Southwestern Brazil in separate areas of varying sizes (Linares-Palomino et al., 2011). The Caatinga phytogeographic domain is a seasonally dry tropical forest (SDTF) (Pennington et al. 2009) endemic to Brazil. It represents one of the largest semiarid regions in South America, occurring over approximately 800,000 km² in Northeastern Brazil (Silva et al. 2017). Caatinga has an extended dry period in which rainfall is scarce (Silva et al. 2017), and as a result, most of the vegetation is deciduous (Prado 2003). The seasonality and rainfall distribution, associated with elevated temperatures and highly variable edaphic conditions, drive a diverse spectrum of Caatinga phytogeographic formations (Sampaio 1995; Moro et al. 2015). At least 13 different physiognomies span a broad range of woody plant densities, and this is collectively referred to as the Caatingas (Prado 2003). Their flora is considered the most diverse for SDTFs on Earth (Silva et al. 2019), harboring 4,891 species, 1,232 genera, 176 families of flowering plants, and 298 endemic species (Flora 2020) of 31 endemic genera (Queiroz et al. 2017). Fabaceae is the most species-rich family, with 490 species among 112 genera (Fernandes et al. 2020).

Many groups of herbivorous insects occur in the Caatinga, and among them are the leaf chewing (e.g., Coleoptera, Orthoptera, Lepidoptera, and Phasmatodea;), sap-sucking (mostly Hemiptera), wood-boring, and gall-inducing insects (Santos et al. 2011; Leal et al. 2018; Costa and Araújo 2019). Among these groups of herbivores, gall-inducing insects are noteworthy for being the herbivorous insect guild with a higher specificity for their host plants (Joy and Crespi 2007; Carneiro et al. 2009; Grandez-Rios et al. 2015). In the Neotropical region, gall inducers are poorly known taxonomically, and most of the species are new to science (Gagné and Jaschhof 2021), especially in the SDTF. Studies about gall-inducing insects in the Caatinga are recent, and the first studies were carried out about ten years ago (see Santos et al. 2011). In a recent review of the state of the art of gall-inducing insect studies in Brazil, Caatinga is identified as one of the least studied and most promising ecosystems (Araújo et al. 2019). In this context, there are still many gaps in the knowledge of patterns of galling insect diversity in the Brazilian Caatinga.

In the present study, we investigated the diversity patterns of host plants and galling insect species in the Brazilian Caatinga. No previous study has been published toward understanding general patterns in host plant richness and galling insect species throughout this ecosystem. In this context, the present work aimed to: a) compile the information available in the literature about inventories of insect galls and their host plants communities in the Caatinga; b) quantitatively and qualitatively analyze the richness of host plants and galling insect species; c) estimate the number of threatened species of host plants and galling insects; d) estimate the potential number of galling insect species for Caatinga; and e) describe the number of galling species per host plant, where each host plant had been classified in, single-hosts plants with only one gall species, multi-hosts those plants with two or more galls per plant and, super-hosts plants that hosted numerous galling insect species.

Material and Methods

1. Data collection for host plant and galling morphotypes

We conducted a comprehensive literature search for data about galling insects and their host plants in the Brazilian Caatinga. We searched potential studies through online academic databases, such

as Google Scholar, JStor, ISI Web of Knowledge, Scielo, and Scopus. To search the online databases, we used the following terms which were combined in different ways: “galling insect,” “insect gall,” “inventories,” “richness,” “Brazil,” “Brazilian,” “seasonally dry tropical forest,” and “Caatinga.” Searches were conducted only in Portuguese and English. Our data compilation was focused on community studies, such as checklists and inventories of host plants and gall-inducing insects; therefore, we discarded paper that contained case studies involving botany, ecology, and zoology. Our data set results from the compilation of gall-inducing insects and their host plants recorded in different localities in the Brazilian Caatinga. From our searches, the data were obtained from nine papers from 2011 to 2019: Santos et al. (2011), Carvalho-Fernandes et al. (2012), Luz et al. (2012), Costa et al. (2014a), Costa et al. (2014b), Nogueira et al. (2016), Alcântara et al. (2017), Brito et al. (2018), and Costa and Araújo (2019).

We checked the name spelling and authorship, as well as the update of the host plant species according to Flora do Brasil 2020 (<http://floradobrasil.jbrj.gov.br>) (Flora do Brazil 2020). For this analysis, we used host plant species with valid, specific names according to Flora 2020 (156 records). For plant family classification, we used the APG IV (Chase et al. 2016). Then, we discarded all records with taxonomic uncertainty in the following situations: a) plants not identified at any taxonomic level (species, genus, or family; 32 records, 12%); b) plants that were identified only at the family level, or without genus identification, or in which the host plant was only referred to as “sp.” (35 records, 13%); c) plants identified at the family and genus level followed by “sp.” (41 records, 15%); and d) plants identified as *conferatum* (cf.), in this case, species were not confirmed to specific species (6 records, 2%). These data were discarded for the main analyses, and they were used later only to see the additive effects of the number of genera and families in the diversity of host plants (details in the Supplementary Material). Once the identity of the plant was confirmed, we obtained the following variables: the number of records (the number of studies that reported plant species), and the number of plant species by genus and family.

For gall-inducing insects, the taxon was not included because most studies do not provide their identification. Instead, they use gall morphology as a phenotypic trait to separate gall morphospecies. Then, for each study, we recorded the number of galling insects morphotypes by plant species. From there, we had a general list of plant species and the number of galling insect species found for each of the nine studies evaluated. We observed a lack of standardization in the description of gall morphotypes (Isaías et al. 2013), which led us to adopt some procedures to reduce the redundancy of their number. Most of the plant species (74 ssp., 74%) had only one record, so for them, we had no problems, because only a single author described the morphotypes. However, 26% (26 ssp.) of the plant species had from two to seven gall-inducing insect records for the same plant. In this situation, we use the following approach: a) when two or more authors reported equal numbers of gall morphotypes for the same species of plant, we arbitrarily selected one record and deleted the other records; and b) when two or more authors reported different numbers of gall morphotypes for the same plant species, we selected the plant record with the highest number of gall-inducing insect species. We used this criterion because plants with more reported galling insect species are expected to be more representative of the galling insect community. Although we understand

the limitations of this choice, we believe it is the best method to use, since there is little data available on galling species to directly estimate the number of galling insects by host plant species.

2. Subset of data with only host plant species of Caatinga

Our pre-analysis showed that the host plant community had many typical Cerrado species, which are not normally found in the Caatinga. This was because some studies were done in ecotone areas between Caatinga and Cerrado, and because of the presence of some phytophysiognomies in the Cerrado that occur within the Caatinga domain. Because of this, we wanted to know the additive effects that the plants of the Cerrado have on the diversity and data set of plants and galling insects of the Caatinga. We excluded plant species that occur in the Cerrado with no distribution in Caatinga. Thus, a subset of data with only host plants with distribution in the Caatinga was obtained from Fernandes et al. (2020). These authors published the most recent, comprehensive, and taxonomically verified checklist of the flowering plant species occurring in the Caatinga of Northeast Brazil, with 3,347 species, 962 genera, and 153 families.

3. Data collection for Cecidomyiidae species

After obtaining the host plant list, we manually added the described galling insect species associated with those host plant species. We searched for the new species of gall inducers in the same online academic databases used to produce the host plant list, changing only the terms which were combined among the following words (in Portuguese and English): “Cecidomyiidae,” “gall,” “new species,” “Brazil,” and “Caatinga” combined with the names of host plant species. The most important insect families referred to as gall inducer in the nine inventories in the Caatinga was Cecidomyiidae (Diptera), the richest gall inducer in the world (Gagné and Jaschhof 2021). Because of this, we also searched for cecidomyiids species in two sources: a) in the fifth edition of “A Catalogue of the Cecidomyiidae of the World” (Gagné and Jaschhof 2021); and b) in the Museu Nacional of Universidade Federal do Rio de Janeiro (MNRJ) and Museu de Zoologia of Universidade de São Paulo (MZUSP) databases, where the new species of cecidomyiid are deposited in Brazil. We discarded all records of gall inducers without identification to the species level (144 records). Once the gall inducers associated with the host plant species was confirmed, we obtained the following variables: the number of records (the number of studies that reported gall inducers associated with host plants), the number of gall inducers by host plant species, genus, and family, and the most frequent gall inducers species associated with the host plant species, genus, and family.

4. Statistical analysis

We made some descriptive statistical analyses for an overview of the data. First, we provide a rarefaction curve for species, genera, and families of gall-inducing insects number in relation to the number of studies. We also graphically represent the distribution of the number of gall-inducing insects' species by host plant species in relation the total number of host plant species and the estimated of the total number of galling insect species in the Caatinga. And finally, we ranked plots of the number of host plant records, host plant species galling insect species for 32 host plant families in the Caatinga.

Results

1. Host plants and their galling insects

Overall, we found 254 records (153 records to valid species) among 100 species, 72 genera, and 32 families of host plants in the nine studies compiled for the Brazilian Caatinga (Table S1, Table S2). When we compared our results with the taxa of species of plants of the Caatinga (*sensu* Flora do Brasil 2020), we registered that only 2% of the species (4,891 spp. total), 6% of the genera (1,232 genera total), and 18% of the families (176 families total) of all plants of the Caatinga host galling insects. The asymptote showed that families tend to stabilize with an increase in the number of studies. However, for species and genera, a greater increment of 160 studies is expected to stabilize the curve (Figure 1).

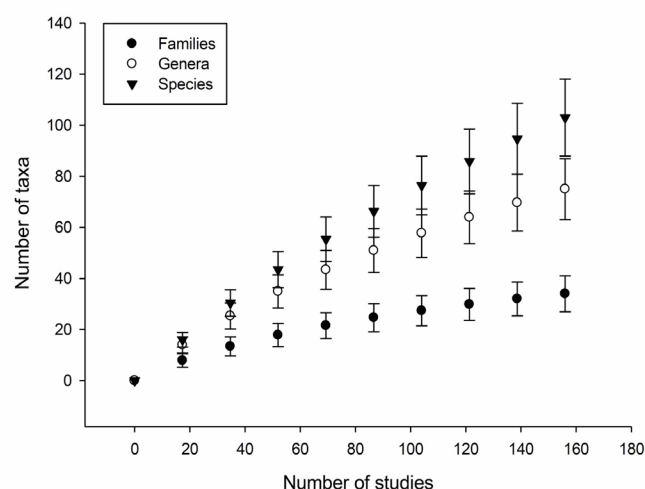


Figure 1. Rarefaction curves for species, genera, and families of host plants of galling insects by study number in the Caatinga. Bars dotted indicate 95% confidence intervals.

Additionally, we found two species that are vulnerable to extinction (VU) according to the Red List of Brazilian Flora, and they were: *Apuleia leiocarpa* (Vogel) J.F. Macbr. (Fabaceae; two gall morphotypes) and *Manilkara dardanoi* Ducke (Sapotaceae; one gall morphotype). Behind the species of host plants, three species are in the near-threatened (NT) category (*Bowdichia virgilioides* Kunth [Fabaceae], *Handroanthus impetiginosus* [Mart. ex DC.] Mattos [Bignoniaceae], and *Handroanthus impetiginosus* [Mart. ex DC.] Mattos [Bignoniaceae]), each with one galling morphotype.

In relation to galling insects, we found a total of 156 morphospecies of insect galls associated with 100 host plants in the Caatinga (Table S1). This equates to a ratio of 1.56. Twelve species of described cecidomyiids were associated with 10 host plant species from eight families that occur in the Caatinga (Table S3). Three species were of the family Fabaceae (*Andira humilis* Mart. ex Benth., *Bauhinia brevipes* Vogel and *Mimosa tenuiflora* [Willd.] Poir.) and one was of each family: Annonaceae (*Duguetia furfuracea* [A. St.-Hil.] Saff.), Calophyllaceae (*Calophyllum brasiliense* Cambess.), Caryocaraceae (*Caryocar brasiliense* Cambess.), Combretaceae (*Combretum leprosum* Mart.), Malpighiaceae (*Byrsonima intermedia* A. Juss.), Malvaceae (*Waltheria indica* L.), and Sapotaceae

(*Pouteria torta* [Mart.] Radlk.) (see the association in the Table S3). This represents only 7% of the morphotypes estimated on 10% of the host plants reported in Caatinga.

The single hosts, plants with only one gall species, were the most common hosts, comprising 74% (74 spp.) of all host plants. Multi-hosts, those plants with two or more galls per plant, represented 26% (26 spp.) of all hosts (Figure 2a). In addition, some plant species, called super-hosts, hosted numerous galling insect species. In this study, we considered those plants within our data sets with the highest number of galling insects. For example, two species were 2% of all plant species, and they were: *Copaifera langsdorffii* Desf. (nine spp.), and *Croton jacobinensis* Baill. (eight spp.; Table S1). Despite few species, these plant species had a large number of gall morphotypes, with about 11% of all gall species (17 spp.; Figure 2b).

The four most frequently recorded species represented about 13.1% of the total records: *Copaifera langsdorffii* Desf. (Fabaceae), *Bauhinia brevipes* Vogel (Fabaceae), *Bauhinia pulchella* Benth. (Fabaceae), and *Combretum leprosum* Mart. (Combretaceae) (Table 1, Table S4). Of

the 100 species, 66 spp. (ca. 43.1%) were registered only once, 23 spp. (ca. 30.1%) were registered twice, and seven species (ca. 17.3%) were registered three times (Table S1). It is no accident that five species of inducers identified for the Caatinga were found in Fabaceae, two in *Bauhinia brevipes* and *Mimosa tenuiflora*, and one in *Andira humilis*.

Bauhinia was the plant genus that stood out because of the large number of records (N = 14, 9.2%). When the number of species per genera was considered, it showed that the most specious genera are *Croton* (N = 6 spp., 6%), *Bauhinia* (N = 5 spp., 5%), and *Eugenia* (N = 4 spp., 4%; Table 1, Table S4). In addition, another three genera (*Bauhinia*, *Croton*, and *Copaifera*) together had around 25% (39 spp.) of the total number of registered gall-inducing insect species, and 69 other genera, about 75% (117 galls spp.; Table 1, Table S3).

Fabaceae was the plant family with the most records (N = 59, 38.6%) (Figure 3a). When the number of host plant species and galling species per family was considered, it showed that Fabaceae was also the most specious family. It corresponded to one third the number of species

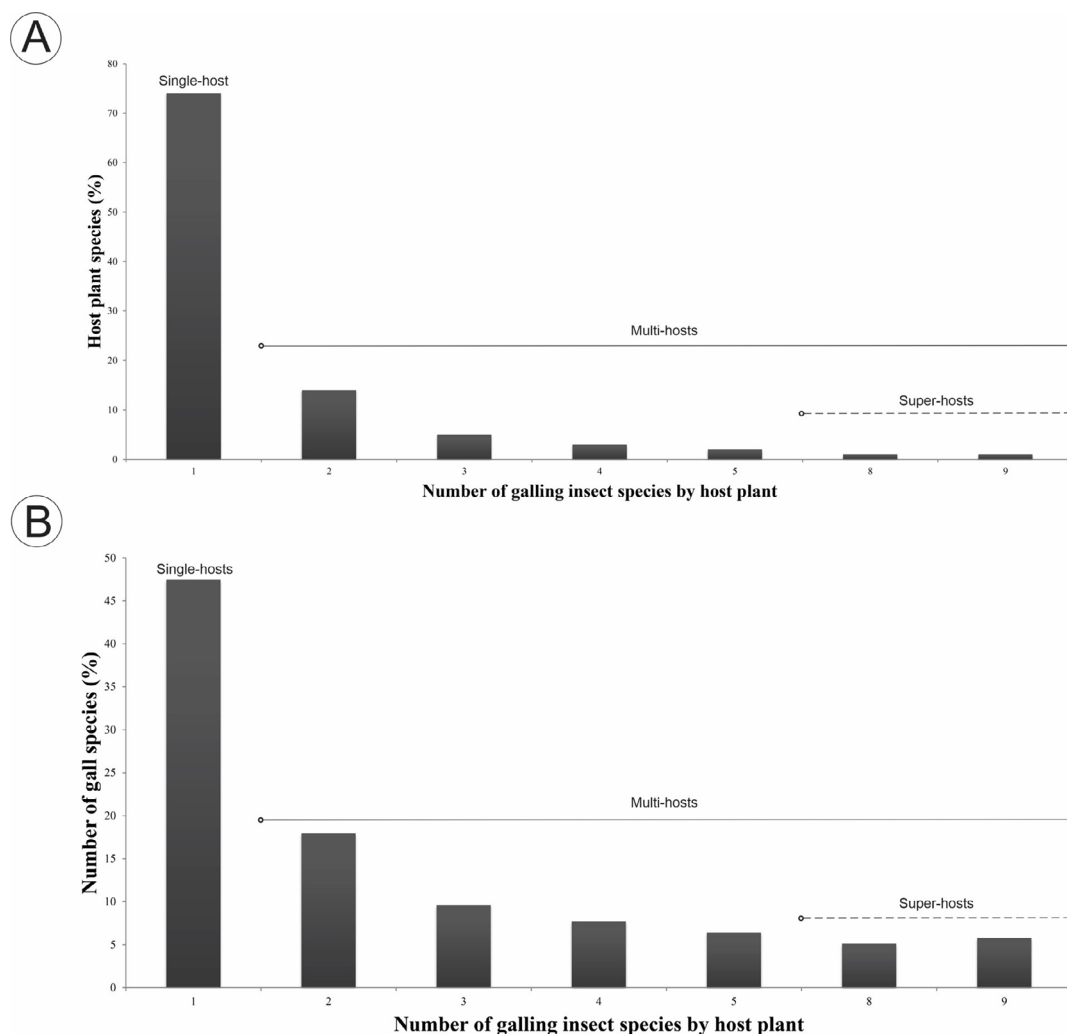


Figure 2. Distribution of the number of galling insect species by host plant species (A) and the estimated of the total number of galling insect species (B) in the Caatinga. We highlight in this figure the single-hosts, plant species with only one insect species; the multi-hosts, plant species with two or more gall species; and the super-hosts, plant species with eight or more galls. The implications for single-, multi- and super-host were put into the results and discussed posteriorly.

Table 1. Genera with more host plant species and more galling insect species in the Caatinga and the ratio of the estimated number of gall species by host plants. The complete list of all 72 genera was placed as supplementary data (Supplementary Table 3).

Host genera	Host plant richness (%)	Number of galling species (%)	Number of galling species/host plant species
<i>Croton</i>	6 (6%)	14 (9.0%)	2.3
<i>Bauhinia</i>	5 (5%)	16 (10.3%)	3.2
<i>Eugenia</i>	4 (4%)		1.8
<i>Copaifera</i>		9 (5.8%)	9.0
Subtotal	16 (16%)	46 (29.5%)	
Others (68)	84 (84%)	110 (70.5%)	
Total	100 (100%)	156 (100%)	

found (N = 30 spp., 30%) (Figure 3b) and approximately 40% of the number of galls morphospecies quantified (61 galls spp.; Figure 3c).

We compiled 12 cecidomyid gall midge species associated with the plants that occurred in the Caatinga: *Anisodiplosis waltheriae* Maia, *Asphondylia byrsonimae* Maia & Couri, *Asphondylia microcapillata* Maia, *Schizomyia macrocapillata* Maia, *Bruggmanniella duguetiae* Urso-Guimarães & Amorim, *Contarinia gemmae* Maia, *Houardodiplosis rochae* Tavares, *Lopesia andirae* Garcia, Lima, Calado & Urso-Guimarães, *Lopesia mimosae* Maia, *Lopesia pernambucensis* Maia, *Prodiptosis floricola* (Felt), and *Youngomyia matogrossensis* Proença & Maia. Nevertheless, only four cecidomyid species are recorded in this biome: *Houardodiplosis rochae* Tavares, *Lopesia mimosae* Maia, *Lopesia pernambucensis* Maia, and *Schizomyia macrocapillata* Maia.

2. Only Caatinga

We then removed the Cerrado species from the data set and analyzed only the species that occur in the Caatinga, according to Fernandes et al. (2020). We found that Cerrado plants contributed with 22% to the diversity of host plants and 19% to the richness of galling insects. The results showed that the plant richness fell to 78 spp. (2% of Caatinga flora), 58 genera (6%), and 25 families of host plants (16%), and 127 gall morphospecies. Of these species, 10 host plants spp. (*Annona leptopetala* [R.E.Fr.] H.Rainer [Annonaceae], *Calliandra macrocalyx* Harms [Fabaceae], *Cnidocolus quercifolius* Pohl [Euphorbiaceae], *Croton adamantinus* Müll.Arg. [Euphorbiaceae], *Croton blanchetianus* Baill. [Euphorbiaceae], *Croton jacobinensis* Baill. [Euphorbiaceae], *Manihot dichotoma* Ule [Euphorbiaceae], *Mimosa pseudosepiaria* Harms [Fabaceae], *Neocalyptocalyx longifolium* [Mart.] Cornejo & Iltis [Capparaceae], and *Varronia leucocephala* [Moric.] J.S.Mill. [Boraginaceae]) and another 20 galling insect spp. were endemic to the Caatinga.

Discussion

In our results, we found a low number of species of host plants (100 spp.) and gall-inducing insects (156 spp.). When we compared this result with other biomes, the difference was clearer. In a recent study, Cintra et al. (2020) compiled information from several localities in the Cerrado using community studies about plant-galling insect species and their host plants. They found 505 host plant species and 996 gall-inducing insect species. We propose three arguments to explain this pattern. First, it is likely that the number of galling insect inventories for the Caatinga is under-sampled, as indicated by the rarefaction curve.

The number of inventories in the Caatinga is low compared to more studied biomes, such as the Cerrado and Atlantic Forest (Araújo et al. 2019). For example, for the Cerrado, there are more than 32 inventories (Cintra et al. 2020) against just nine for the Caatinga. This low number of inventories in the Caatinga can generate a shortlist of the number of species of host plants. However, when we compare the average number of galls morphotypes found in the inventories, the results showed that the richness of galling insects in the Caatinga is smaller than in other biomes. In this study, on average number of galls/inventories for the Caatinga was 41 (N = 9 inventories), while for the Cerrado was 49 (N = 32 inventories) (Cintra et al. 2020; see also Araújo et al., 2019).

Our second argument is that the Caatinga has a relatively smaller number of plant species compared to the Cerrado, for instance. The Caatinga flora has 4,891 valid spp., 1,232 genera, and 176 families of flowering plants. Meanwhile, the Cerrado flora has 12,420 valid spp., 1,662 genera, and 187 families (Flora do Brazil 2020). In absolute numbers, this difference is remarkable because the Cerrado has 2.5 times more species than the Caatinga. Therefore, with less potential host species for radiation and galling insect diversification, the Caatinga accumulates few species of host plants and, consequently, few galling insect species.

A third argument is that the Caatinga is a seasonally dry tropical forest, in other words, a semiarid environment, with low rainfall, often irregular rains and with marked seasonality (Marengo et al. 2017). During the dry season in the Caatinga, many species lose their leaves, constituting a strongly deciduous vegetation (Queiroz et al. 2017). Insects induce galls preferentially on the leaves (e.g., about 60%, see Maia et al. 2014), compared to other organs of the host plant. Consequently, there is a drastic reduction in the quantity and quality of resources available to galling insects, e.g., meristematic tissues. This may be the main limiting factor for limited adaptive radiation from galling insects in the Caatinga. Andrade et al. (2020) monitored herb communities for three weeks in the Caatinga to determine if rainfall reduction decreases insect herbivory. They found no leaf damaged by galling insects, even in the driest plots. According to Mendonça (2001), the deciduousness is a relevant factor in the colonization and performance rates of galling insects and can determine the patterns of diversity and distribution of this species.

Besides, the Caatinga is a xeric environment with high hygrothermal stress. Fernandes and Price (1988, 1991) argue that the richness of gall-inducing insects is higher in hygrothermal stressed habitats (hygrothermal stress hypothesis). Then, according to this hypothesis, we expected to find in Caatinga a high richness of host plants and gall-

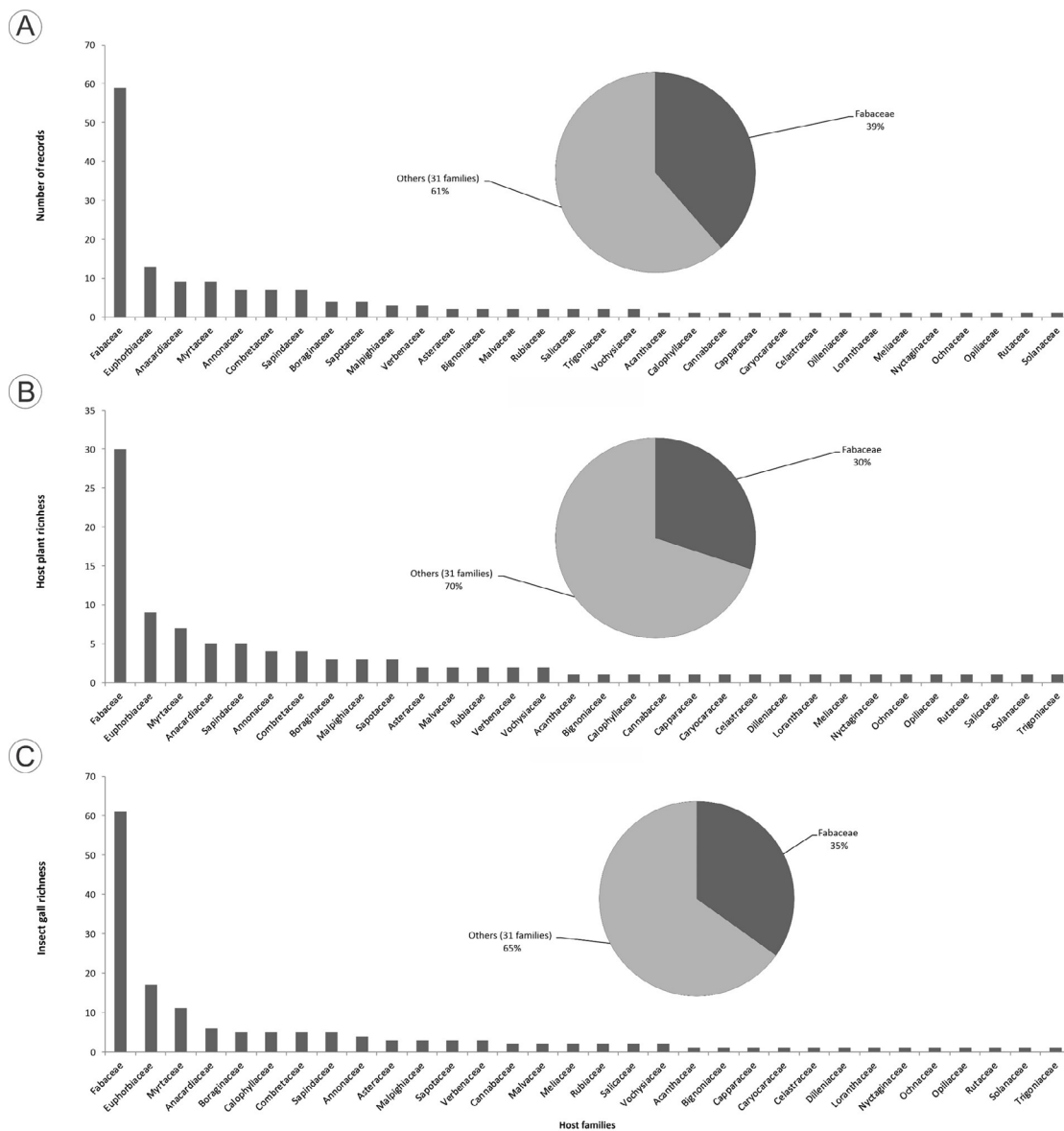


Figure 3. Rank plots of the number of host plant records (A), host plant species (B) and galling insect species (C) for 32 host plant families in the Caatinga. In the right corner of each figure, we show the proportion of Fabaceae, the family with the highest numbers of records, host plant and insect galls in relation to others 31 families.

inducing insect, but these predictions were not confirmed in this study nor in a study by Andrade et al. (2020) that expected more leaf damage by endogenous insects (leaf-mining and galling insects) in drier areas (with high hygrothermal stress) in the Caatinga. We argue that herbivory patterns by galling insects in the Caatinga are mainly ruled from bottom to top, being the aridity a strong factor that reduces plant resources to endophytic herbivores. For instance, during the transition between climatic seasons in the Caatinga, many plants still feature incomplete leaf replacement or deciduous characteristics (Albuquerque et al. 2012). Although, other abiotic factors (soil quality and water stress) and biotic factors (plant age, plant density, and natural enemies) may also affect gall-inducing species richness at different scales (Fernandes and Price 1991; Lara and Fernandes 1996; Ribeiro et al. 1998).

Only four gall midge species have been recorded in the Caatinga. If we consider that there are about 260 species of Cecidomyiidae occurring

in Brazil (V.C. Maia *personal communication*), we notice that the Caatinga fauna includes less than 2% of the Brazilian richness. However, the occurrence of the other eight gall midge species is possible, because they induce galls on host plants reported in the Caatinga. Furthermore, two other species could be added to this list: *Anadiplosis caetetensis* Tavares, 1920, and *Styraxdiplosis caetetensis* Tavares, 1918, as both were described from Caetité (Bahia), a municipality occupied by Caatinga and Atlantic Forest. If we consider only the gall inducers recorded in the areas of Caatinga, only four species will remain in the list: *Schizomyia macrocapillata* Maia, 2005, *Houardodiplosis rochae* Tavares, 1925, *Lopesia mimosae* Maia, 2009, and *Lopesia pernambucensis* Maia, 2009, which is only 3% of the gall-inducing insects. We estimated that 93% of the gall-inducing species recorded in the Caatinga inventories are still undescribed, so further studies to identify the most representative groups of gall inducers for this biome

are needed. For this, it is necessary to obtain all the stages of life for these gall-inducing insects.

In our study, Fabaceae were the most recurrent plant family with a total of 30 host plant species and 61 gall-inducing insect species. This is the most species-rich family detected in STDFs (Pennington et al. 2000; Meguro et al. 2007; Fernandes et al. 2020). Several Brazilian inventories in different biomes also point out the Fabaceae as one of the plant families with the highest number of insect galls (reviewed in Araújo et al. 2019). Additionally, host plant family size may be an important factor for the regional prediction of gall-inducing insect species richness (Araújo 2011), once gall-inducing insects generally exhibit opportunistic adaptive irradiation (Price 2005).

The *Copaifera langsdorffii*, is a tropical arboreal tree, with the richest fauna of gall inducers insects (with 23 morphotypes) (Costa et al. 2010). Because of this, *C. langsdorffii* is considered a super host species. In our study, we recorded nine galling species for *C. langsdorffii*. Super host species may be responsible for the differences in local and regional patterns of gall-inducing insect richness (Fernandes and Price 1988) and, as such, represent keystone species for galling insects (Araújo et al. 2013).

Conclusions

Our results showed a low number of species of host plants and gall-inducing insects for the Brazilian Caatinga, and we discussed this pattern with three arguments. Initially, it is probable that the numbers of galling insect inventories for the Caatinga were under-sampled. When we compared the average number of galls found in the inventories, the results showed that the richness of galls in the Caatinga is smaller than in other biomes, such as the Cerrado and Atlantic Forest (Araújo et al. 2019). Secondly, we argue that the Caatinga has a relatively smaller number of plant species, which means that, with less potential host species for radiation and galling insect diversification, the Caatinga accumulates few species of host plants and, consequently, galling insect species. Lastly, we argue that the Caatinga is a seasonally dry tropical forest (Marengo et al. 2017), and so during the dry season in the Caatinga, many species lose their leaves, showing a strongly deciduous vegetation (Queiroz et al. 2017). For this reason, according to Mendonça (2001), the deciduousness represents a relevant factor in the colonization and performance rates of galling insects and can determine the patterns of diversity and distribution of this species.

Supplementary Material

The following online material is available for this article:

Supplementary Material - Beyond: an analysis by genus and families of unidentified host plant species.

Table S1 - The complete list of all 100 host plant in the Caatinga Biome, with number of records (NR), proportion of number of records [NR(%)], number of galling insect species (NGI), and proportion of galling insect species [NGI (%)].

Table S2 - Study location and coordinates of inventories about gall-inducing insects and their host plants in Caatinga Biome.

Table S3 - The list of 12 known gall inducers associated with the host plant species of the Caatinga Biome, including additional information.

Table S4 - The complete list of all 72 host plant genera in the Caatinga Biome, with number of records (NR), proportion of number

of records [NR(%)], number of host plant species (NHP), proportion of host plant species [NHP (%)], number of galling insect species (NGI), proportion of galling insect species [NGI (%)] and also the ratio of the number of gall species by host plants (NGI/NHP)

Acknowledgements

The authors thank Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) [CNPq grants 312752/2018-0 (J.C.S) and fellowships: 140128/2019-0 (F.C.F.C.) and 140158/2018-9 (H.V.)].

Authors Contributions

Fernanda Cristina Franco Cintra: Substantial contribution in the concept and design of the study, contribution to data collection, contribution to data analysis and interpretation, contribution to manuscript preparation, adding intellectual content.

Valéria Cid Maia: Contribution to data collection, and data interpretation.

Maria Virginia Urso-Guimarães: Contribution to data collection, and data interpretation.

Walter S. de Araújo: Contribution to data interpretation adding intellectual content.

Marco Antônio Alves Carneiro: Contribution to data analysis.

Henrique Venâncio: Contribution to data collection, and data interpretation.

Wanessa R. Almeida: Contribution to data collection, contribution to data analysis and interpretation.

Jean Carlos Santos: Substantial contribution in the concept and design of the study contribution to data collection, contribution to data analysis and interpretation and contribution to critical revision.

Conflicts of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

- ALBUQUERQUE, U.P., ARAÚJO, E.L., EL-DEIR, A.C.A., LIMA, A.L.A., SOUTO, A., BEZERRA, B.M., FERRAZ, E.M.N., FREIRE, E.M.X., SAMPAIO, E.V.S.B., LAS-CASAS, F.M.G., MOURA, G.J.B., PEREIRA, G.A., MELO, J.G., RAMOS, M.A., RODAL, M.J.N., SCHIEL, N., LYRA-NEVES, R.M., ALVES, R.R.N., AZEVEDO-JÚNIOR, S.M., JÚNIOR, W.R.T. & SEVERI, W. 2012. Caatinga revisited: Ecology and conservation of an important seasonal dry forest. *Sci. World. J.* 205182.
- ALCÂNTARA, J.A., SOUZA, E.B. & BRAGA, P.E.T. 2017. Ocorrência e caracterização de galhas em duas áreas do noroeste do Ceará, Brasil. *Natureza online*. 15(1):33–40.
- ANDRADE, J.F., ALVARADO, F., CARLOS SANTOS, J. & SANTOS, B.A. 2020. Rainfall reduction increases insect herbivory in tropical herb communities. *J. Veg. Sci.* 31(3):487–496.
- ARAÚJO, W.S. 2011. Size, age, and composition: Characteristics of plant taxa as diversity predictors of gall-midges (Diptera: Cecidomyiidae). *Rev. Biol. Trop.* 59(4):1599–1607.
- ARAÚJO, W.S., FERNANDES, G.W. & SANTOS, J.C. 2019. An overview of inventories of gall-inducing insects in Brazil: Looking for patterns and identifying knowledge gaps. *An. Acad. Bras. Cienc.* 91(1):1–19.

- ARAÚJO, W.S., SCARELI-SANTOS, C., GUILHERME, F.A.G. & CUEVAS-REYES, P. 2013. Comparing galling insect richness among Neotropical savannas: Effects of plant richness, vegetation structure and super-host presence. *Biodivers. Conserv.* 22(4):1083–1094.
- BRITO, G.P., COSTA, E.C., CARVALHO-FERNANDES, S.P. & SANTOS-SILVA, J. 2018. Riqueza de galhas de insetos em áreas de caatinga com diferentes graus de antropização do estado da Bahia, Brasil. *Iheringia Ser. Zool.* 108:e2018003.
- CARNEIRO, M.A.A., BRANCO, C.S.A., BRAGA, C.E.D., ALMADA, E.D., COSTA, M.B.M., MAIA, V.C. & FERNANDES, G.W. 2009. Are gall midge species (Diptera, Cecidomyiidae) host-plant specialists? *Rev. Bras. Entomol.* 53(3):365–378.
- CHASE, M.W. et al. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Bot. J. Linn. Soc.* 181(1):1–20.
- CARVALHO-FERNANDES, S.P., ALMEIDA-CORTEZ, J.S.F. & NUNES, A.L. 2012. Riqueza de galhas entomógenas em áreas antropizadas e preservadas de caatinga. *Rev. Árvore.* 36(2):269–277.
- CINTRA, F.C.F., ARAÚJO, W.S., MAIA, V.C., URSO-GUIMARÃES, M.V., VENÂNCIO, H., ANDRADE, J.F., CARNEIRO, M.A.A., DE ALMEIDA, W.R. & SANTOS, J.C. 2020. Plant-galling insect interactions: a data set of host plants and their gall-inducing insects for the Cerrado. *Ecology* 101(11):e03149.
- COSTA, E.C., CARVALHO-FERNANDES, S.P. & SANTOS-SILVA, J. 2014a. Galhas de insetos em uma área de transição caatinga-cerrado no Nordeste do Brasil. *Sitientibus. Sér. Ciênc. Biol.* 141–9.
- COSTA, E.C., CARVALHO-FERNANDES, S.P. & SANTOS-SILVA, J. 2014b. Galhas entomógenas associadas à Leguminosae do entorno do riacho Jatobá, Caetité, Bahia, Brasil. *R. Bras. Bioci.* 12:115–120.
- COSTA, F.V., FAGUNDES, M. & NEVES, F.S. 2010. Arquitetura da planta e diversidade de galhas associadas à *Copaifera langsdorffii* (Fabaceae). *Ecol. Austral.* 20:9–17.
- COSTA, K.C.S. & ARAÚJO, W.S. 2019. Distribution of gall-inducing arthropods in areas of deciduous seasonal forest of Parque da Sapucaia (Montes Claros, MG, Brazil): effects of anthropization, vegetation structure and seasonality. *Pap. Avulsos. Zool.* 59: e20195931. 0205/2019.59.31
- FERNANDES, G.W. & PRICE, P.W. 1988. Biogeographical gradients in galling species richness - Tests of hypotheses. *Oecologia* 76(2):161–167.
- FERNANDES, G.W. & PRICE, P.W. 1991. Comparison of tropical and temperate galling species richness: the roles of environmental harshness and plant nutrient status. In *Plant-animal interactions: evolutionary ecology in tropical and temperate regions.* (P.W. PRICE, T.M. LEWINSON, G.W. FERNANDES & W.W. BENSON, eds) John Wiley, New York, p 91–115.
- FERNANDES, M.F., CARDOSO, D. & QUEIROZ, L.P. 2020. An updated plant checklist of the Brazilian Caatinga seasonally dry forests and woodlands reveals high species richness and endemism. *J. Arid. Environ.* 174:104079.
- FLORA DO BRAZIL 2020 (2020) Jardim Botânico do Rio de Janeiro. <http://floradobrasil.jbrj.gov.br/>. Accessed 26 May 2020
- GAGNÉ, R.J. & JASCHHOF, M. 2021. A Catalogue of Cecidomyiidae (Diptera) of the World. 5rd Edition. Digital. 813 pp.
- GRANDEZ-RIOS, J.M., GARCÍA-VILLACORTA, R., CUEVAS-REYES, P. & DE ARAÚJO, W.S. 2015. Insectos inductores de Agallas en América Latina: Ecología, Importancia y Nuevas Perspectivas. *Rev. Biol. Neotrop.* 12(2):92.
- ISAÍAS, R. M. S., CARNEIRO, R. G. S., OLIVEIRA, D. C. & SANTOS, J. C. 2013. Illustrated and Annotated Checklist of Brazilian Gall Morphotypes. *Neotrop. Entomol.* 42: 230–239.
- JOY, J.B. & CRESPI, B.J. 2007. Adaptive radiation of gall-inducing insects within a single host-plant species. *Evolution* 61(4):784–795.
- LARA, A.C.F. & FERNANDES, G.W. 1996. The highest diversity of galling insects: Serra do Cipó, Brazil. *Biodivers. Lett.* 3(3):111–114.
- LEAL, I.R., LOPES, A. V., MACHADO, I.C. & TABARELLI, M. 2018. Plant-animal interactions in the Caatinga: Overview and perspectives. In *Caatinga: The Largest Tropical Dry Forest Region in South America.* (J.M.C. SILVA, I.R. LEAL & M. TABARELLI eds) Springer International Publishing, p.255–278.
- LINARES-PALOMINO, R., OLIVEIRA-FILHO, A.T. & PENNINGTON, R.T. 2011. Neotropical Seasonally Dry Forests: Diversity, Endemism, and Biogeography of Woody Plants. In *Seasonally Dry Tropical Forests.* (R. DIRZO, H.S. YOUNG, H.A. MOONEY & G. CEBALLOS eds) Island Press/Center for Resource Economics, p.3–21.
- LUZ, G.R., FERNANDES, G.W., SILVA, J.O., NEVES, F.S. & FAGUNDES, M. 2012. Galhas de insetos em habitats xérico e méxico em região de transição Cerrado-Caatinga no norte de Minas Gerais, Brasil. *Neotrop. Biol. Conserv.* 7(3):171–187.
- MAIA, V.C., RODRIGUES, A.R., ASCENDINO, S. & BOGGI, M. 2014. The insect gall collection of the Museu Nacional/Universidade Federal do Rio de Janeiro: biome cerrado, rupestrian fields. *Braz. J. Biol.* 207(3):207–217.
- MARENGO, J.A., TORRES, R.R. & ALVES, L.M. 2017. Drought in Northeast Brazil—past, present, and future. *Theor. Appl. Climatol.* 129:1189–1200.
- MEGURO, M., PIRANI, J.R., MELLO-SILVA, R. & CORDEIRO, I. 2007. Composição Florística e Estrutura das Florestas Estacionais Decíduas Sobre Calcário a Oeste da Cadeia do Espinhaço, Minas Gerais, Brasil. *Bol. Botânica.* 25(2):147.
- MENDONÇA, M.S. 2001. Gallling insect diversity patterns: the resource synchronisation hypothesis. *Oikos* 95(1):171–176.
- MORO, M.F., SILVA, I.A., DE ARAÚJO, F.S., LUGHADHA, E.N., MEAGHER, T.R. & MARTINS, F.R. 2015. The role of edaphic environment and climate in structuring phylogenetic pattern in seasonally dry tropical plant communities. *PLoS ONE* 10(3).
- NOGUEIRA, R.M., COSTA, E.C., CARVALHO-FERNANDES, S.P. & SANTOS-SILVA, J. 2016. Insect galls from Serra Geral, Caetité, BA, Brazil. *Biota. Neotrop.* 16:1–10.
- PENNINGTON, R.T., LAVIN, M. & OLIVEIRA-FILHO, A. 2009. Woody plant diversity, evolution, and ecology in the tropics: Perspectives from seasonally dry tropical forests. *Annu. Rev. Ecol. Evol. Syst.* 40:437–457.
- PENNINGTON, R.T., PRADO, D.E. & PENDRY, C.A. 2000. Neotropical seasonally dry forests and Quaternary vegetation changes. *J. Biogeogr.* 27(2):261–273.
- PRADO, D. E. 2003. As caatingas da América do Sul. In *Ecologia e conservação da Caatinga.* (I. R. LEAL, M. TABARELLI & J. M. C. SILVA eds) Editora Universitária da UFPE, p. 3–73.
- PRICE, P.W. 2005. Adaptive radiation of gall-inducing insects. *Basic. Appl. Ecol.* 6(5):413–421.
- QUEIROZ, L.P., CARDOSO, D., FERNANDES, M.F. & MORO, M.F. 2017. Diversity and evolution of flowering plants of the Caatinga Domain. In *Caatinga: The Largest Tropical Dry Forest Region in South America.* (J.M.C. SILVA, I.R. LEAL & M. TABARELLI eds) Springer International Publishing, p. 23–63.
- RIBEIRO, K.T., MADEIRA, J.A. & MONTEIRO, R.F. 1998. Does flooding favour galling insects? *Ecol. Entomol.* 23(4):491–494.
- SAMPAIO, E.V.S.B. 1995. Overview of the Brazilian Caatinga. In *Seasonally Dry Tropical Forests.* (S.H. BULLOCK & H.A. MOONEY eds) Cambridge University Press, Cambridge, p. 35–63.
- SANTOS, J.C., ALMEIDA-CORTEZ, J.S. & FERNANDES, G.W. 2011. Diversidade de insetos indutores de galhas em brejos de altitude de Pernambuco, Nordeste do Brasil. *Brazilian. J. Biol.* 71:47–56.
- SILVA, J.L.S.E., CRUZ-NETO, O., PERES, C.A., TABARELLI, M. & LOPES, A.V. 2019. Climate change will reduce suitable Caatinga dry forest habitat for endemic plants with disproportionate impacts on specialized reproductive strategies. *PLoS ONE* 14(5): e0217028.
- SILVA, J.M.C., BARBOSA, L.C.F., LEAL, I.R. & TABARELLI, M. 2017. The Caatinga: Understanding the Challenges. In *Caatinga: The Largest Tropical Dry Forest Region in South America.* (J.M.C. SILVA, I.R. LEAL & M. TABARELLI eds) Springer International Publishing, p.3–19.

Received: 20/04/2021

Accepted: 27/10/2021

Published online: 17/12/2021