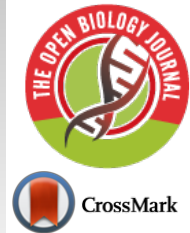




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RESEARCH ARTICLE

Insights into Super-host Plant Species of Gall-ing Insects in the Neotropical Region

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Abstract:

Background:

The term ‘super host’ plant is often used in the literature surrounding plant-galling interactions, but the different contexts in which the term is used generates doubt and confusion due to the absence of a systematic definition of the term’s meaning.

Objective:

In this study, we used 60 well-defined plant-galling assemblages to propose a systematic definition of super-host plants at the local and regional level. In addition, we investigated factors that explain the number of gall-ing species per host plant at different geographic scales.

Methods:

Plant-galling assemblages were compiled from an extensive literature review on insect gall inventories carried out in Brazil.

Results:

We found 888 host plant species belonging to 94 families and 340 genera hosting 2,376 insect gall morphotypes. At a local scale, 33.2% of host plant species harbored one insect gall morphotype and 12.2% hosted two gall morphotypes, making up 45.4% of the host plant species in each locality. At the regional scale, 51.5% of host plant species harbored one insect gall morphotype, and 17.9% of host plant species hosted two gall morphotypes, corresponding to 69.4% of all host plant species. Based on the average number of gall-ing species per plant species, we classified the plant species into: 1) Host species; 2) Multi-host species and 3) Super-host species. The super-host plant species that showed the greatest richness of gall morphotypes at the local level were *Baccharis reticularia* and *Adenocalymma neoflavidu*. Furthermore, we found a positive relationship between plant life-form architectural complexity and the number of gall-ing species at the local level. At the regional scale, we registered five super-host species (*Guapira opposita*, *Protium heptaphyllum*, *Copaifera langsdorffii*, *Myrcia splendens*, and *Byrsonima sericea*) which hosted 21 or more insect gall morphotypes. The number of gall-ing species per host plant species at the regional scale was influenced positively by geographic distribution rank and number of biomes in which each species of the plant occurs.

Conclusion:

The present study stands out as the first of its kind to provide a systematic standardization for the super-host plants and to investigate factors influencing these species.

Keywords: Ecological interactions, Gall-ing arthropods, Herbivory, Insect galls, Plant-animal interactions, Neotropical region.

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1. INTRODUCTION

Interactions involving host plants and gall-ing insects are

among the most diverse and specialized in nature [1, 2]. In the Neotropical region, a great diversity of plant-galling interactions has been studied in recent years [3 - 5]. Estimates indicate that more than 15,400 species of gall-ing insects and more than 29,000 species of host plants exist in the neotropics [3]. Gall-ing species tend to be species-specific with their hosts

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[6], but host plant species can host a variable number of galling insect species [7]. In most cases, the number of galling insect species per host plant species is usually one or two, although some host species can house more than 20 different galling species [8, 9].

In studies investigating plant-galling interactions in the Neotropical region, the term ‘super-host’ is frequently used to designate plant species that host a high richness of galling species [10]. For example, Costa *et al.* [11] defined *Copaifera langsdorffii* (Fabaceae) as a super-host because it houses 23 galling species. In a separate study, this same host species was recorded as a super-host while hosting 17 galling species [12]. *Copaifera oblongifolia*, another congeneric species was also named a super-host by Fagundes *et al.* [13] and Coutinho *et al.* [14], hosting 15 galling species. Goetz *et al.* [15] named *Piper aduncum* (Piperaceae) and *Mikania glomerata* (Asteraceae) super-hosts, harboring eight and six galling species, respectively. In another study, Maia and Oliveira [16] used the term super-host to describe *Guapira opposita* (Nyctaginaceae) which hosted four galling insect species. In an extreme case, Ribeiro *et al.* [17] defined *Moquiniastrum pulchrum* (Asteraceae) as a super-host plant, by housing two galling species. These examples illustrate how the term ‘super-host’ is frequently used in galling insect studies, often in an indiscriminate and non-standardized way.

The number of herbivorous insects hosted by host plants can be influenced by several factors at different scales [18]. At the local scale, studies have pointed to plant traits such as life-form as influencing the distribution of galling species, with trees usually hosting greater galling insect diversity than non-arboreal plants [19]. These results agree with the hypothesis that host plants with higher architectural complexity house more insect herbivore species [20, 21]. At the regional scale, the plant’s geographic range has been hypothesized as an important predictor of the diversity of herbivorous insects hosted by a plant species [18]. This pattern can be explained by the fact that hosts with a wide distribution have contact with a greater diversity of herbivores, which promotes the accumulation of more interactions throughout their distribution [22]. The aforementioned factors (amongst others), may potentially explain the occurrence of super-host plant species, though this remains a knowledge gap of plant-galling interactions.

In this context, the standardized definition of the term ‘super-host’ and the investigation of factors influencing the occurrence of these species are important to guide studies of insect gall diversity in neotropical environments. In this study, we propose a definition to differentiate super-host plants at the local and regional level using a dataset compiled from the literature surrounding plant-galling inventories in Brazil. We aim to answer the following questions: 1) What defines super-host plants at the local level? 2) Do super-host plants vary locally? 3) Are there factors that explain the occurrence of super-host taxa at the local level? 4) What defines super-host plants at the regional level? 5) Are there factors that explain the occurrence of super-host taxa at the regional level?

2. METHODS

2.1. Data Compilation

We carried out a comprehensive literature search for studies reporting assemblages of gall insects associated with

their host plant in the SciVerse Scopus, Portal Capes, and Google Scholar databases (until 2017), using the following combinations of keywords: (plant*) and (galls*) and (interaction* or web*) and (survey* or list*). It is important to note that we compiled only inventories of the richness of host plants and galling insects, and we did not consider literature focused on a single species of plant or galling insect, to ensure that all studies included had searched for all galls occurring in the community. Thus, only those studies with plant-gall insect assemblages that met all of the following criteria were included in our study: 1) At least 3 host plant species; 2) At least 3 host plants hosting a minimum of 3 galling insect species (*i.e.*, insect gall morphotypes); and 3) An indication that all plants could potentially be utilized by the gall insect assemblages in the list (*i.e.*, no spatial mismatch). Overall, 60 local plant-galling assemblages were selected from 31 studies (Supplementary Material 1). The latitudinal distribution of the plant-galling assemblages ranged from 1°20’ S to 29°28’ S, and their altitudes ranged from 10 to 1,860 m.a.s.l.

2.2. Plant Species

For each local plant-galling assemblage we checked the synonymy of host plant using "The Plant List" database (www.theplantlist.org). We also used additional information, such as the Tropicos (www.tropicos.org) databases to refine a list of each family, genus, and host plant species where they were sampled. Host plants that were taxonomically determined only at the genus level (*i.e.*, species identified as “sp.”) were also added to the list.

2.2.1. Local and Regional Gall Morphospecies Diversity

We used compiled data to calculate the richness of insect galls at local and regional levels. At the local level, we considered the number of gall morphotypes described in each host plant species within the community. For the categorization of the morphotypes, we considered the original morphological (*i.e.*, plant organ, shape, color, and pilosity) description made by the authors of the studies. We did not consider the size of galls as an important character in our study due to the high variability in this characteristic. The use of morphotypes as a surrogate for the species of galling insects is widespread in the literature due to the high specificity of galls and the lack of taxonomic studies of gallers [5]. At the regional level, we considered the sum of unique morphotypes on each host plant species in the different plant-galling communities.

It is important to emphasize that our measure of gall richness at the regional level, is strongly dependent on sampling effort for each host plant species because plant species that have occurred in several communities are more likely to accumulate more galls over space [5]. However, we believe that as we adopt the criterion of compiling only studies that inventoried the entire plant community, this effect can be mitigated. Besides, the authors did not look a priori at specific plant species, they collected information for all plants in the community. Thus, it is expected that the plant species that are registered in different studies are species with wide distribution between habitats and localities.

2.3. Data Analyses

At the regional level, we used a Generalized Linear Model (GLM) to investigate plant-related factors (life-forms, endemism, geographic range, biome occurrence, vegetation occurrence) on the galling species richness. Predictive variables were ordered as ordinal (sequential) variables. For the plant life-form architectural complexity, we used the following categories: 1 = herb, 2 = liana, 3 = shrub and 4 = tree. With regards to endemism, we considered plant species with occurrence only in Brazil as endemic and species occurring in Brazil and other countries as non-endemic. The categories used for the geographical distribution area were: 1 = distribution restricted to a small area/locality, 2 = biome (in a single state), 3 = biome (occurring in several states), 4 = Brazil (occurring in different biomes in the same state) and 5 = Brazil (occurring in different biomes and states). For vegetation, we used the following categories: 1 = grassland, 2 = savanna and 3 = forest. We used this ranking because there is an increasing gradient of structural complexity (in terms of biomass, tree cover, and height of vegetation) grassland < savanna < forest. We also accounted for the number of biomes within which each plant species occurs. At the local level, we also used a GLM to investigate whether galling species richness is influenced by plant life-form using the same life-form categories as above. All of the models were built using the error of Poisson distribution. All statistical analyses were performed in R version 3.4.1 [23].

3. RESULTS

A total of 888 host plant species belonging to 94 families and 340 genera were analyzed hosting 2,376 insect gall morphotypes. The most important host plant family was Fabaceae, hosting 291 (12.2%) insect gall morphotypes, follo-

wed by Asteraceae (263; 11.0%), Myrtaceae (260; 10.9%), Melastomataceae (126; 5.3%), Malpighiaceae (111; 4.6%), and Burseraceae (100; 4.2%). The most important of host plant genera were *Myrcia* (Myrtaceae) with 106 (4.4%), *Protium* (Burseraceae) with 85 (3.6%), *Eugenia* (Myrtaceae) with 84 (3.5%), *Baccharis* (Asteraceae) with 81 (3.4%), and *Byrsonima* (Malpighiaceae) with 78 (3.2%) insect gall morphotypes.

At a local scale, $33.2 \pm 10.5\%$ of host plant species in each locality harbored one insect gall morphotype and $12.2 \pm 4.8\%$ hosted two gall morphotypes, totaling 45.4% of the host plant species (Fig. 1; Table 1). Considering all host plant species, the mean number of gall morphotypes per plant species was 2.67 ± 3.33 . We considered plant-species with more than double of this mean (*i.e.*, six or more species) as super host plants at a local scale (Table 2), which correspond to less than 1% of host plant species in each locality. For a given locality, the maximum number of insect gall morphotypes per plant species ranged between 3 and 10. Plant species that hosted between three and six insect gall morphotypes were categorized as multi-host plant species (Table 2). Super-host plants at the local level were represented by 23 species occurring across 24 localities (Table 3). The species that hosted the most gall morphotypes at individual sites were *Baccharis reticularia* with 10 insect gall morphotypes in the Parque Estadual do Itacolomi and *Adenocalymma neoflavidum* (Bignoniaceae) with nine gall morphotypes in the Floresta Nacional Saracá-Taquera. Host plant species more frequently listed in inventories of galling insects were *Guapira opposita* (eight studies), *Eremanthus erythropappus* (Asteraceae) (three studies) and *Protium heptaphyllum* (three studies) (Table 3). We found a positive relationship between the life-form and the number of galling species at the local level (Deviance = 14.46, df = 1779, $p < 0.001$).

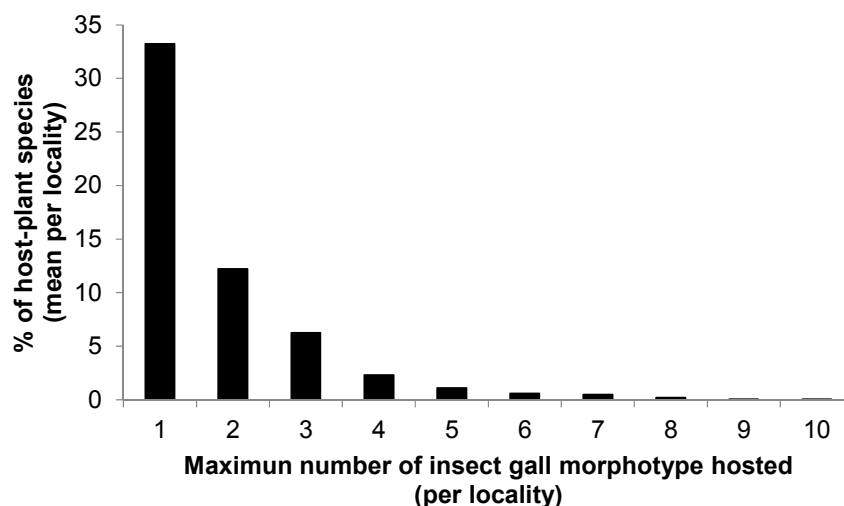


Fig. (1). Percentage of host plant species hosting different richness of galling species (maximum number of insect gall morphotype hosted).

Table 1. Range of galling insect richness (insect gall morphotypes) per host plant species.

Range (Gall Morphotypes per Plant Species)	Percent of Host Plant Species per Locality			
	Mean	SD	Max	Min
1	33.2	10.6	63.6	12.5
2	12.2	4.8	21.3	0
3	6.2	3.2	17.1	0
4	2.3	2.1	8.3	0
5	1.1	1.6	5.7	0
6	0.6	1.1	4.2	0
7	0.5	1.2	6.3	0
8	0.2	0.6	2.9	0
9	0.0	0.2	1.6	0
10	0.0	0.2	1.8	0

Table 2. Categorization of super-host plant species at the local and regional scales.

Ecological Scale	Range of Richness of Insect Gall Morphotypes	Category of Host Plant Species
Local scale	1 to 3	Host plant species
	3 to 6	Multi-host plant species
	6 or more	Super-host plant species
Regional scale	1 to 3	Host plant species
	6 to 20	Multi-host plant species
	21 or more species	Super-host plant species

Table 3. List of super-host plants at the local scale based on Brazilian plant-galling inventories.

Super-host Plant Species	Plant Family	Number of Insect Gall Morphotypes	Locality	References
<i>Baccharis pseudomyriocephala</i>	Asteraceae	10	Parque Estadual do Itacolomi	Carneiro <i>et al.</i> [24]
<i>Adenocalymma neoflavidum</i>	Bignoniaceae	9	Floresta Nacional Saracá-Taquera	Araújo <i>et al.</i> [25]
<i>Baccharis platypoda</i>	Asteraceae	8	Parque Estadual do Brigadeiro	Coelho <i>et al.</i> [26]
<i>Protium heptaphyllum</i>	Burseraceae	8	Serra de São José Cachoeira do Mangue	Maia and Fernandes [27]
<i>Guapira opposita</i>	Nyctaginaceae	8	Bertioga	Maia [28]
<i>Mikania biformis</i>	Asteraceae	8	Bertioga	Maia [28]
<i>Guapira opposita</i>	Nyctaginaceae	8	Maricá	Maia [28]
<i>Copaifera langsdorfii</i>	Fabaceae	8	Cachoeira da Lua	Maia [29]
<i>Guapira opposita</i>	Nyctaginaceae	8	Ilha da Marambaia - Armação	Rodrigues <i>et al.</i> [30]
<i>Baccharis reticularia</i>	Asteraceae	7	Parque Estadual do Itacolomi	Carneiro <i>et al.</i> [24]
<i>Baccharis platypoda</i>	Asteraceae	7	RPPN do Caraça	Carneiro <i>et al.</i> [24]
<i>Baccharis reticularia</i>	Asteraceae	7	RPPN do Caraça	Carneiro <i>et al.</i> [24]
<i>Byrsonima coccolobifolia</i>	Malpighiaceae	7	RPPN do Caraça	Carneiro <i>et al.</i> [24]
<i>Protium sagotianum</i>	Burseraceae	7	Platô Bacaba - Porto de Trombetas	Maia [31]
<i>Myrcia splendens</i>	Myrtaceae	7	Bertioga	Maia [28]
<i>Ocotea pulchella</i>	Lauraceae	7	Bertioga	Maia [28]
<i>Eugenia astringens</i>	Myrtaceae	7	Jurubatiba	Maia [28]
<i>Guapira opposita</i>	Nyctaginaceae	7	Jurubatiba	Maia [28]
<i>Mikania biformis</i>	Asteraceae	7	Guaratuba	Maia <i>et al.</i> [32]
<i>Myrcia splendens</i>	Myrtaceae	7	Praia do Itaguapé	Maia <i>et al.</i> [32]
<i>Guapira opposita</i>	Nyctaginaceae	7	Estação Biológica de Santa Lúcia	Maia <i>et al.</i> [33]
<i>Mikania laevigata</i>	Asteraceae	7	Parque Natural Municipal São Lourenço	Maia <i>et al.</i> [33]
<i>Protium heptaphyllum</i>	Burseraceae	7	Mata Semicaudicifolia - UFG	Silva <i>et al.</i> [34]
<i>Styrax pohlii</i>	Styracaceae	7	Mata Semicaudicifolia - UFG	Silva <i>et al.</i> [34]
<i>Guapira opposita</i>	Nyctaginaceae	7	Ilha da Marambaia - Sitio	Rodrigues <i>et al.</i> [30]

(Table 3) contd....

Super-host Plant Species	Plant Family	Number of Insect Gall Morphotypes	Locality	References
<i>Eremanthus erythropappus</i>	Asteraceae	6	Parque Estadual do Itacolomi	Carneiro et al. [24]
<i>Byrsonima coccolobifolia</i>	Malpighiaceae	6	Parque Estadual do Biribiri	Carneiro et al. [24]
<i>Eremanthus erythropappus</i>	Asteraceae	6	RPPN do Caraça	Carneiro et al. [24]
<i>Eremanthus erythropappus</i>	Asteraceae	6	Serra do Ouro Branco	Carneiro et al. [24]
<i>Copaifera langsdorffii</i>	Fabaceae	6	Campus Pampulha - UFMG	Fernandes et al. [35]
<i>Copaifera langsdorffii</i>	Fabaceae	6	Serra de São José Cachoeira do Mangue	Maia and Fernandes [27]
<i>Myrcia multiflora</i>	Myrtaceae	6	Restinga de Carapebus	Maia [36]
<i>Miconia stenostachya</i>	Melastomataceae	6	Platô Bacaba - Porto de Trombetas	Maia [31]
<i>Tetragastris panamensis</i>	Burseraceae	6	Platô Bacaba - Porto de Trombetas	Maia [31]
<i>Myrcia sylvatica</i>	Myrtaceae	6	Cachoeira da Lua	Maia [29]
<i>Eugenia astringens</i>	Myrtaceae	6	Carapebus	Maia [29]
<i>Myrcia multiflora</i>	Myrtaceae	6	Carapebus	Maia [29]
<i>Calophyllum brasiliense</i>	Calophyllaceae	6	Vale das Borboletas	Maia [29]
<i>Guapira opposita</i>	Nyctaginaceae	6	Praia do Itagaré	Maia et al. [32]
<i>Psychotria vellosiana</i>	Rubiaceae	6	Estação Biológica de Santa Lúcia	Maia et al. [33]
<i>Guapira opposita</i>	Nyctaginaceae	6	Parque Natural Municipal São Lourenço	Maia et al. [33]
<i>Protium heptaphyllum</i>	Burseraceae	6	Reserva Ecologica de Saltinho	Santos et al. [37]

Table 4. List of super-host plants at the regional scale based on Brazilian plant-galling inventories.

Super-Host Plant Species	Plant Family	Number of Insect Gall Morphotypes	References
<i>Guapira opposita</i>	Nyctaginaceae	40	Bregonci et al. [38], Maia [36], Rodrigues et al. [30], Maia et al. [32], Santos et al. [37], Maia and Carvalho-Fernandes [39], Maia and Silva [40], Maia [28], Maia et al. [33].
<i>Protium heptaphyllum</i>	Burseraceae	35	Maia [36], Maia and Fernandes [27], Santos et al. [37], Silva et al. [34], Fernandes et al. [41], Maia and Carvalho-Fernandes [39], Maia [29], Santana and Isaias [42].
<i>Copaifera langsdorffii</i>	Fabaceae	27	Maia [29], Santos et al. [43], Fernandes et al. [35], Urso-Guimarães and Scareli-Santos [44], Coelho et al. [45], Fernandes et al. [46], Maia and Fernandes [27], Silva et al. [34], Luz et al. [47], Santana and Isaias [42].
<i>Myrcia splendens</i>	Myrtaceae	23	Rodrigues et al. [30], Coelho et al. [45], Fernandes et al. [46], Maia et al. [32], Maia [29], Santana and Isaias [42].
<i>Byrsonima sericea</i>	Malpighiaceae	22	Bregonci et al. [38], Maia [36], Oliveira and Maia [48], Rodrigues et al. [30], Santos et al. [37], Maia and Carvalho-Fernandes [39], Maia and Silva [40], Maia [28].

At the regional scale, 51.5% of host plant species harbored one insect gall morphotype, and 17.9% of host plant species hosted two gall morphotypes, corresponding to 69.4% of all host plant species in this study. We considered plant-species with more than double the mean of insect gall morphotypes per host plant species (2.67 ± 3.33) as multi-host plants (*i.e.*, host plants with six or more insect gall morphotypes) (Table 2), which correspond to 91 host plant species with a mean of 10.20 ± 5.82 gall morphotypes. Plant species with more than double the mean number of galls of multi-host plants (*i.e.*, 21 or more insect gall morphotypes) were considered as super-host plants (Table 2). This classification resulted in a total of five super-host plant-species at the regional level: *Guapira opposita* (40 insect gall morphotypes), *Protium heptaphyllum* (35), *Copaifera langsdorffii* (27), *Myrcia splendens* (23), and *Byrsonima sericea* (22) (Table 4). Super-host plant species had a mean of 29.4 ± 7.82 insect gall morphotypes. The number of galling insect species per host plant species at the regional scale was influenced positively by life-form (Deviance = 5.13, $df = 845$, $p = 0.02$), geographic distribution rank (Deviance =

68.93 , $df = 841$, $p < 0.001$), number of biomes (Deviation = 74.41, $df = 840$, $p < 0.001$) and by increased vegetation complexity (Deviation = 87.14, $df = 823$, $p < 0.001$).

4. DISCUSSION

In this study, we adopted the reasoning that super-host species are those that have a greater variety of insect galls compared to the average galling species richness per plant species occurring within the community. The criterion adopted in our study indicates that super-hosts at a local level are the species with six or more galling species, which represent twice the average diversity of galling species per plant species. Our criterion at the regional level was more rigorous because on a macroscale all plant species accumulate more species of herbivorous insects than on a local scale [18]. Thus, we refer to the plant species that at the regional level have an intermediate species richness of insect galls as multi-hosts and we consider super-hosts to be only those species that have more than twice the average galling species richness of multi-hosts. Thus, at the regional level, we considered super-host plants to be the only

species that hosted 21 or more species of galling insects. Based on the criteria presented here, our study represents the first systematized definition of super-host plants both at the community (local scale) and the macrogeographic level (regional scale).

Our approach revealed, from a wide range of data, that the species of super-host plants can vary greatly over different geographic scales. Although 23 species can be considered super-hosts at the local level (*i.e.*, had six species of galling insects or more), we observed that some species are frequently listed as super-hosts such as *Guapira opposita*. We also found that at the local scale plants with a high diversity of insect galls tend to be more complex, that is, they have arboreal life-form [19]. The architectural complexity of trees tends to be higher compared to other plant life-forms because trees have higher height, the number of shoots, branches, and leaves with the crown volume [20]. In addition, the trees are larger and have greater biomass than other life-forms which allows a greater accumulation of herbivorous insects [19]. These different parameters positively influence the richness of insect galls as they represent a greater availability of resources (*i.e.*, biomass) and oviposition sites (*i.e.*, types of tissues) for galling insects [11, 19]. At the regional level, super-host plant (*i.e.*, had 21 species of galling insects or more) were represented by only five plant species, with *Guapira opposita* and *Protium heptaphyllum* that hosted the highest numbers of insect galls. Our results show that, in general, super-host plants on a macrogeographic scale are those with a greater range of distribution and that occur in a greater number of biomes.

The plant *Guapira opposita* was also the super-host species at the local level most frequently recorded in our database, being recorded eight times. This species is a tree widely distributed across South America, and in Brazil is registered in Amazonia, Caatinga, Cerrado, and Atlantic Forest [49]. With regards to vegetation types, *Guapira opposita* is registered in riparian forest, seasonal semideciduous forest, rainforest, mixed rainforest, restinga, and vegetation on rocky outcrops [49]. In Brazil, this species has been registered as a super-host in areas of restinga and coastal vegetation [28, 30, 33]. The compiled database showed that this super-host plant presents an elevated alpha diversity of galling insects across several Brazilian locations. This can be explained by their structural architecture, given that trees tend to host a greater diversity of herbivorous insects compared to other plant life-forms [20]. Besides, we hypothesized that the great diversity of galling insects associated with *Guapira opposita* is related to the adaptive irradiation of gall-midges (Cecidomyiidae, Diptera) on this plant. For example, there is evidence of the occurrence of many species of *Bruggmania* associated with this host [50], which indicates that processes of sympatric speciation happened during the evolutionary history of this system.

Other important super-host plant species at the local scale were *Eremanthus erythropappus* and *Protium heptaphyllum*, which were each recorded three times. *Eremanthus erythropappus* is an endemic tree in Brazil that occurs in Cerrado and Atlantic Forest, and being frequently recorded in rocky savanna, typical savanna, riparian forest, and seasonal semideciduous forest [51]. This species has been recorded as a super-

host in different areas of the Espinhaço Range [24]. *Protium heptaphyllum* is a neotropical tree registered in Brazil, in the Amazonia, Caatinga, Cerrado, and Atlantic Forest. Among the types of vegetation that *Protium heptaphyllum* occurs are campinarana, riparian forest, terra firme forest, rainforest, restinga, and savannah [52]. This species has been registered as a super-host in the Atlantic Forest [37], Semideciduous forest [34], and Cerrado [27].

At the regional level, *Guapira opposita* with 40 insect gall morphotypes and *Protium heptaphyllum* with 35, were the most important super-host plants. As previously indicated, these plant species were also the most recurrent super-hosts at the local level. This result indicates that in addition to a high alpha diversity locally, these super-host species also have a high beta diversity, due to the replacement of galling species throughout space [53]. Our results also indicate that breadth of geographic distribution and number of biomes positively influenced the number of galling insect species per host plant species at the regional scale. In a broad review, Nyman [22] argues that hosts with a wide range of distribution tend to accumulate more species of herbivorous insects as a result of added possibilities for local adaptation. The high numbers of galling species hosted by *Guapira opposita* and *Protium heptaphyllum* can be explained by the wide-ranging distribution of these species across the Neotropical region [49, 52], given that the two species occur across different countries in Latin America, and are registered in several biomes in Brazil.

CONCLUSION

Based on our initial questions and results, we conclude that in tropical and sub-tropical Brazil: 1) Super-host plants at the local level are species that host six or more galling species; 2) Species of super-host plants vary widely between communities, but some species are recurrently registered as super-hosts, such as *Guapira opposita*; 3) Plant life-form influences the richness of insect galls that they host, with super-hosts tending to be arboreal; 4) On a regional scale, super-host plants are those species that host 21 or more galling insect species; 5) Species of super-host plants at the regional level tend to have a wider range of geographic distribution and occur across several different biomes. The present study stands out as the first to provide a systematic standardization for super-host plants and to investigate factors influencing these species.

AUTHORS' CONTRIBUTIONS

JMGR and WSA designed the experiment. JMGR and CGHP performed the data compilation. WSA performed statistical analyses. All authors prepared the manuscript.

ETHICAL APPROVAL AND CONSENT TO PARTICIPATE

Not applicable.

HUMAN AND ANIMAL RIGHTS

No animals/humans were used for studies that are the basis of this research.

CONSENT FOR PUBLICATION

Not applicable.

AVAILABILITY OF DATA AND MATERIALS

The data that support the findings of this study are available from the corresponding author [W.S.A] on request.

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None.

CONFLICT OF INTEREST

The authors declare no conflict of interest, financial or otherwise.

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REFERENCES

- [1] Araújo WS, Freitas ÉVD, Kollár J, *et al.* Host specialization in plant-galling interactions: Contrasting mites and insects. *Diversity (Basel)* 2019; 11(10): 180. [<http://dx.doi.org/10.3390/d11100180>]
- [2] Harris MO, Pitzschke A. Plants make galls to accommodate foreigners: Some are friends, most are foes. *New Phytol* 2020; 225(5): 1852-72. [<http://dx.doi.org/10.1111/nph.16340>] [PMID: 31774564]
- [3] Grandez-Rios JM, García-Villacorta R, Cuevas-Reyes P, De Araújo WS. Insectos inductores de agallas en américa latina: Ecología, importancia y nuevas perspectivas. *Rev Biol Neotrop* 2015; 12(2): 92. [<http://dx.doi.org/10.5216/rbn.v12i2.32619>]
- [4] Araújo WS. 30 years of research on insect galls in Brazil: A scientometric review. *Pap Avulsos Zool* 2018; 58e20185834 [<http://dx.doi.org/10.11606/1807-0205/2018.58.34>]
- [5] Araújo WS, Fernandes GW, Santos JC. An overview of inventories of gall-inducing insects in Brazil: Looking for patterns and identifying knowledge gaps. *An Acad Bras Cienc* 2019; 91(1)e20180162 b [<http://dx.doi.org/10.1590/0001-3765201920180162>] [PMID: 30916155]
- [6] Coelho Kuster V, Costa Rezende U, Fernandes Cardoso JC, Santos Isaias RM, Coelho de Oliveira D. How galling organisms manipulate the secondary metabolites in the host plant tissues? A histochemical overview in neotropical gall systems. Reference series in phytochemistry Co-evolution of secondary metabolites. Springer International Publishing 2019; pp. 1-20. [http://dx.doi.org/10.1007/978-3-319-76887-8_29-1]
- [7] Araújo WS, Scareli-Santos C, Guilherme FAG, Cuevas-Reyes P. Comparing galling insect richness among Neotropical savannas: Effects of plant richness, vegetation structure and super-host presence. *Biodivers Conserv* 2013; 22(4): 1083-94. [<http://dx.doi.org/10.1007/s10531-013-0474-8>]
- [8] Fernandes GW, Carneiro MAA, Lara ACF, *et al.* Galling insects on neotropical species of *Baccharis* (Asteraceae). *Trop Zool* 1996; 9(2): 315-32. [<http://dx.doi.org/10.1080/03946975.1996.10539315>]
- [9] Fagundes M, Xavier RCF, Faria ML, Lopes LGO, Cuevas-Reyes P, Reis-Junior R. Plant phenological asynchrony and community structure of gall-inducing insects associated with a tropical tree species. *Ecol Evol* 2018; 8(22): 10687-97. [<http://dx.doi.org/10.1002/ece3.4477>] [PMID: 30519398]
- [10] Araújo WS, Moreira LT, Falcão LAD, *et al.* Superhost plants alter the structure of plant-galling insect networks in neotropical savannas. *Plants* 2019; 8(10): 369. c [<http://dx.doi.org/10.3390/plants8100369>] [PMID: 31554312]
- [11] Costa FV, Fagundes M, Neves FS. Arquitetura da planta e diversidade de galhas associadas à *Copaifera langsdorffii* (Fabaceae). *Ecol Austral* 2010; 20(1): 9-17.
- [12] Fagundes M, Santos ÉMS, Duarte K, *et al.* Diversity of gall-inducing insect associated with a superhost plant species: Plant architecture, resource availability and interspecific interactions. *Biodiversitas J Biol Divers* 2020; 21(3): 1182-9. [<http://dx.doi.org/10.13057/biodiv/d210344>]
- [13] Fagundes M, Barbosa EM, Oliveira JBBS, *et al.* Galling inducing insects associated with a tropical shrub: The role of resource concentration and species interactions. *Ecol Austral* 2019; 29(1): 12-9. [<http://dx.doi.org/10.25260/EA.19.29.1.0.751>]
- [14] Coutinho RD, Cuevas-Reyes P, Fernandes GW, Fagundes M. Community structure of gall-inducing insects associated with a tropical shrub: regional, local and individual patterns. *Trop Ecol* 2019; 60(1): 74-82. [<http://dx.doi.org/10.1007/s42965-019-00010-7>]
- [15] Goetz APM, Luz FA, Toma TSP, Mendonça MS. Gall-inducing insects of deciduous and semideciduous forests in Rio Grande do Sul State, Brazil. *Iheringia Ser Zool* 2018; 108. [<http://dx.doi.org/10.1590/1678-4766e2018015>]
- [16] Maia VC, Oliveira JC. Galhas de insetos da reserva biológica estadual da praia do sul (Ilha Grande, Angra dos Reis, RJ). *Biota Neotrop* 2010; 10(4): 227-37. [<http://dx.doi.org/10.1590/S1676-06032010000400028>]
- [17] Ribeiro AN, Balbi MIPA, Urso-Guimarães MV. Characterization of insect galls from a vegetation area in Altinópolis, São Paulo State, Brazil. *Pap Avulsos Zool* 2019; 59e20195904 [<http://dx.doi.org/10.11606/1807-0205/2019.59.04>]
- [18] Lewinsohn TM, Novotny V, Basset Y. Insects on plants: Diversity of herbivore assemblages revisited. *Annu Rev Ecol Evol Syst* 2005; 36: 597-620. [<http://dx.doi.org/10.1146/annurev.ecolsys.36.091704.175520>]
- [19] Cuevas-Reyes P, Quesada M, Hanson P, Dirzo R, Oyama K. Diversity of gall-inducing insects in a Mexican tropical dry forest: The importance of plant species richness, life-forms, host plant age and plant density. *J Ecol* 2004; 92(4): 707-16. [<http://dx.doi.org/10.1111/j.0022-0477.2004.00896.x>]
- [20] Lawton JH. Plant architecture and the diversity of phytophagous insects. *Annu Rev Entomol* 1983; 28(1): 23-39. [<http://dx.doi.org/10.1146/annurev.en.28.010183.000323>]
- [21] Leite GLD, Veloso RVDS, Zanuncio JC, *et al.* Architectural diversity and galling insects on *Caryocar brasiliense* trees. *Sci Rep* 2017; 7(1): 16677. [<http://dx.doi.org/10.1038/s41598-017-16954-6>] [PMID: 29192234]
- [22] Nyman T. To speciate, or not to speciate? Resource heterogeneity, the subjectivity of similarity, and the macroevolutionary consequences of niche-width shifts in plant-feeding insects. *Biol Rev Camb Philos Soc* 2010; 85(2): 393-411. [<http://dx.doi.org/10.1111/j.1469-185X.2009.00109.x>] [PMID: 20002390]
- [23] R Core Team. A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing 2019. Available from: <https://www.R-project.org/>
- [24] Carneiro MAA, Borges RAX, Araújo APA, Fernandes GW. Insetos indutores de galhas da porção sul da Cadeia do Espinhaço, Minas Gerais, Brasil. *Rev Bras Entomol* 2009; 53(4): 570-92. [<http://dx.doi.org/10.1590/S0085-56262009000400007>]
- [25] Araújo WS, Porfírio-Júnior ÉD, Jorge VA, Espírito-Santo FK. Plantas hospedeiras e galhas entomógenas em sub-bosques de florestas tropicais do Pará, Brasil. *Insul Rev Botânica* 2012; 41: 59-72.
- [26] Coelho MS, Carneiro MAA, Branco CA, Fernandes GW. Insetos indutores de galhas da Serra do Cabral, Minas Gerais, Brasil. *Biota Neotrop* 2013; 13(3): 102-9. [<http://dx.doi.org/10.1590/S1676-06032013000300013>]
- [27] Maia VC, Fernandes GW. Insect galls from Serra de São José (Tiradentes, MG, Brazil). *Braz J Biol* 2004; 64(3A): 423-45. [<http://dx.doi.org/10.1590/S1519-69842004000300007>] [PMID: 15622841]
- [28] Maia VC. Galhas de insetos em restingas da região sudeste do Brasil com novos registros. *Biota Neotrop* 2013; 13(1): 183-209. [<http://dx.doi.org/10.1590/S1676-06032013000100021>]
- [29] Maia VC. Insect galls of São Tomé das Letras (MG, Brazil). *Biota Neotrop* 2013; 13(4): 164-89. [<http://dx.doi.org/10.1590/S1676-06032013000400017>]
- [30] Rodrigues AR, Maia VC, Couri MS. Insect galls of restinga areas of Ilha da Marambaia, Rio de Janeiro, Brazil. *Rev Bras Entomol* 2014; 58(2): 173-97.

- [31] [http://dx.doi.org/10.1590/S0085-56262014000200010] Maia VC. Characterization of insect galls, gall makers, and associated fauna of Platô Bacaba (Porto de Trombetas, Pará, Brazil). *Biota Neotrop* 2011; 11(4): 37-53.
- [32] [http://dx.doi.org/10.1590/S1676-06032011000400003] Maia VC, Magenta MAG, Martins SE. Ocorrência e caracterização de galhas de insetos em áreas de restinga de Bertioga (São Paulo, Brasil). *Biota Neotrop* 2008; 8(1): 167-97.
- [33] [http://dx.doi.org/10.1590/S1676-06032008000100020] Maia V, Cardoso L, Braga J. Insect galls from Atlantic Forest areas of Santa Teresa, Espírito Santo, Brazil: characterization and occurrence. *Bol do Mus Biol* 2014; 33: 47-129.
- [34] [http://dx.doi.org/10.5216/rbn.v1i1.28343] Silva TM, Araújo WS, Santos BB. Ocorrência e caracterização de galhas de insetos em um fragmento de mata semicaducifolia do Campus Samambaia, Goiânia, GO, Brasil. *Rev Biol Neotrop* 2016; 12(1): 26.
- [35] [http://dx.doi.org/10.1590/S0101-81751988000100002] Fernandes GWA, Neto ET, Martins RP. Ocorrência e caracterização de galhas entomógenas na vegetação do campus Pampulha da Universidade Federal de Minas Gerais. *Rev Bras Zool* 1988; 5(1): 11-29.
- [36] [http://dx.doi.org/10.1590/S0101-81752001000200028] Maia VC. The gall midges (Diptera, Cecidomyiidae) from three restingas of Rio de Janeiro State, Brazil. *Rev Bras Zool* 2001; 18(2): 583-629.
- [37] [http://dx.doi.org/10.1590/S0101-81752001000200028] Santos JC, Almeida-Cortez JS, Fernandes GW. Gall-inducing insects from Atlantic Forest of Pernambuco, Northeastern Brazil. *Biota Neotrop* 2012; 12(3): 196-212.
- [38] [http://dx.doi.org/10.1590/S1676-06032012000300020] Bregonci JM, Polycarpo PV, Maia VC. Galhas de insetos do Parque Estadual Paulo César Vinha (Guarapari, ES, Brasil). *Biota Neotrop* 2010; 10(1): 265-74.
- [39] [http://dx.doi.org/10.1590/S1676-06032010000100023] Maia VC, Carvalho-Fernandes SP. Insect galls of a protected remnant of the Atlantic Forest tableland from Rio de Janeiro State (Brazil). *Rev Bras Entomol* 2016; 60(1): 40-56.
- [40] [http://dx.doi.org/10.1016/j.rbe.2015.09.001] Maia VC, Silva LO. Insect galls of Restinga de Marambaia (Barra de Guaratiba, Rio de Janeiro, RJ). *Braz J Biol* 2016; 76(3): 787-95.
- [41] [http://dx.doi.org/10.1590/1519-6984.05314] [PMID: 27097094] Fernandes SPC, Castelo-Branco BP, Albuquerque FA, Brito-Ramos AB, Ferreira ALN, Braga DVV, *et al.* Galhas entomógenas em um fragmento urbano de Mata Atlântica no centro de endemismo de Pernambuco. *Rev Bras Biocienc* 2009; 7(3): 240-4.
- [42] Santana AP, Isaías RMS. Gallling insects are bioindicators of environmental quality in a conservation unit. *Acta Bot Bras* 2014; 28(4): 594-608.
- [43] [http://dx.doi.org/10.1590/0102-33062014abb3510] Santos BB, Ribeiro BA, Silva TM, Araújo WS. Galhas de insetos em uma área de cerrado sentido restrito na região semi-urbana de Caldas Novas (Goiás, Brasil). *Rev Bras Biocienc* 2012; 10(4): 439-45.
- [44] [http://dx.doi.org/10.1590/S1519-69842006000200018] [PMID: 16710528] Urso-Guimarães MV, Scareli-Santos C. Galls and gall makers in plants from the Pé-de-Gigante Cerrado Reserve, Santa Rita do Passa Quatro, SP, Brazil. *Braz J Biol* 2006; 66(1B): 357-69.
- [45] [http://dx.doi.org/10.1590/S0085-56262009000300015] Coelho MS, Almada ED, Fernandes GW, *et al.* Gall inducing arthropods from a seasonally dry tropical forest in Serra do Cipó, Brazil. *Rev Bras Entomol* 2009; 53(3): 404-14.
- [46] [http://dx.doi.org/10.1590/S0085-56262009000300015] Fernandes GW, Araújo RC, Araújo SC, *et al.* Insect galls from savanna and rocky fields of the Jequitinhonha Valley, Minas Gerais, Brazil. *Naturalista* 1997; 22: 221-44.
- [47] [http://dx.doi.org/10.4013/nbc.2012.73.04] Luz GR, Fernandes GW, Silva JO, Neves FS, Fagundes M. Insect galls in xeric and mesic habitats in a Cerrado-Caatinga transition in northern Minas Gerais, Brazil. *Neotrop Biol Conserv* 2012; 7(3): 171-87.
- [48] [http://dx.doi.org/10.4013/nbc.2012.73.04] Oliveira JC, Maia VC. Ocorrência e caracterização de galhas de insetos em áreas de restinga de Bertioga (São Paulo, Brasil). *Arq do Mus Nac Rio* 2005; 63(4): 669-75.
- [49] Sá CFC. Nyctaginaceae in lista de espécies da flora do Brasil Jardim Botânico do Rio de Janeiro Disponível em 2015; 66(4): 1085-113. Available from: <http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB10913>
- [50] [http://dx.doi.org/10.1590/S0101-81751999000200013] Maia VC, Monteiro RF. Espécies cecidógenas (Diptera, Cecidomyiidae) e parasitóides (Hymenoptera) associadas a *Guapira opposita* (Vell.) Reitz (Nyctaginaceae) na Restinga da Barra de Maricá, Rio de Janeiro. *Rev Bras Zool* 1999; 16(2): 483-7.
- [51] [http://dx.doi.org/10.1590/S0101-81751999000200013] Loeuille B. Eremanthus in lista de espécies da flora do Brasil Jardim Botânico do Rio de Janeiro Disponível em 2015. Available from: <http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB5315>
- [52] [http://dx.doi.org/10.1590/S0101-81751999000200013] Daly DC. Burseraceae in lista de Espécies da flora do Brasil Jardim Botânico do Rio de Janeiro Disponível em 2015. Available from: <http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB6593>
- [53] [http://dx.doi.org/10.1590/S1519-566X2010000300009] [PMID: 20676509] Medianero E, Ibáñez A, Nieves-Aldrey JL. The importance of beta diversity in local gall-inducing arthropod distribution. *Neotrop Entomol* 2010; 39(3): 365-70.