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Original Article

Review of the inquilinous fauna associated with insect galls in Brazilian restingas

Revisão da fauna inquilina associada a galhas de insetos em restingas brasileiras

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Abstract

Several records of associated fauna, including parasitoids, inquilines, predators, and successors, have been reported by insect gall inventories in Brazilian restingas. Although most guilds are well established, inquilines have frequently been misinterpreted. In this paper, the inquilinous fauna of insect galls is revised based on five criteria: food habit; coexistence with the inducer; modification of gall tissues or production of new tissues; phylogenetic relationship with the inducer; and mobility. Gall inventories dated from 1988 to 2019 were examined, totaling 16 publications, eight of them with inquiline records. This guild was reported in 53 gall morphotypes in 44 plant species and four morphospecies distributed among 36 genera of 24 host families for a total of 65 records. Most inquilines were repositioned into the cecidophage guild and others into the kleptoparasite guild, resulting in a large reduction in the frequency of inquilines (from 65 to five records), and in first reports of cecidophages and kleptoparasites, with 46 and 13 records, respectively. Cecidophage was the most diverse guild with insects of five orders (Diptera, Coleoptera, Lepidoptera, Hemiptera, and Thysanoptera) while kleptoparasites were represented only by two orders (Diptera and Hymenoptera) and inquiline solely by Hymenoptera. Other results indicate that *Leptothorax* sp. (Formicidae) could be a successor and not an inquiline.

Keywords: Cecidophages, kleptoparasites, gall-inducing insects, Atlantic Forest.

Resumo

Vários registros de fauna associada, incluindo parasitoides, inquilinos, predadores e sucessores são encontrados em inventários de galhas de insetos em restingas brasileiras. Embora a maioria das guildas esteja bem estabelecida, os inquilinos são frequentemente interpretados de forma equivocada. Nesse trabalho, a fauna inquilina de galhas de insetos é revisada com base em cinco critérios: hábito alimentar, coexistência com o indutor, modificação dos tecidos da galha ou produção de novos tecidos, relação filogenética com o indutor e mobilidade. Inventários de galhas publicados entre 1988 e 2019 foram examinados, totalizando 16 artigos, oito deles com registro de inquilinos. Essa guilda foi assinalada em 53 morfotipos de galhas em 44 espécies de plantas e quatro morfoespécies distribuídas em 36 gêneros de 24 famílias vegetais, totalizando 65 registros. A maioria dos inquilinos foi reposicionada na guilda dos cecidófagos e outros na guilda dos cleptoparasitas, resultando em uma grande redução da frequência dos inquilinos (de 65 para cinco registros), e na primeira ocorrência de cecidófagos e cleptoparasitas, com 46 e 13 registros, respectivamente. A guilda dos cecidófagos foi a mais diversa, com insetos de cinco ordens (Diptera, Coleoptera, Lepidoptera, Hemiptera e Thysanoptera), enquanto que os cleptoparasitas foram representados por apenas duas ordens (Diptera e Hymenoptera) e os inquilinos somente por Hymenoptera. Outros resultados indicam que *Leptothorax* sp. (Formicidae) pode ser um sucessor e não um inquilino.

Palavras-chave: Cecidófagos, cleptoparasitas, insetos indutores de galhas, Mata Atlântica.

1. Introduction

Data on the arthropod fauna associated with insect galls have been reported by several inventories in five phytogeographic domains in Brazil: (1) Amazon Forest (Maia, 2011; Carvalho and Motta, 2018), (2) Atlantic Forest (Maia, 2001, 2013, 2014; Maia et al., 2008, 2014; Bregonci et al., 2010; Rodrigues et al., 2014; Maia and Souza, 2013; Carvalho-Fernandes et al., 2016; Maia and Carvalho-Fernandes, 2016; Maia and Mascarenhas, 2017; Ansaloni et al., 2018; Flor et al., 2018; Maia and Siqueira, 2020), (3) Caatinga (Carvalho-Fernandes et al., 2012; Costa et al., 2014; Brito et al., 2018), (4) Cerrado (Fernandes et al., 1988; Urso-Guimarães et al., 2003; Maia and Fernandes, 2004; Araújo et al., 2007; Santos et al., 2010; Araújo et al., 2011; Saito and Urso-Guimarães, 2012; Santos et al., 2012, 2018; Bergamini et al., 2017; Lima and Calado, 2018; Silva et al., 2018 a, b; Vieira et al., 2018;

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Ribeiro et al., 2019), and (5) Pantanal (Ascendino and Maia, 2018). Several gall inventories of Atlantic Forest areas were carried out in restingas, mainly in the state of Rio de Janeiro (Maia, 2001; Rodrigues et al., 2014; Carvalho-Fernandes et al., 2016), but also in Espírito Santo (Bregonci et al., 2010), and São Paulo (Maia et al., 2008). This fauna has been classified as parasitoids, inquilines, gall modifiers, successors, and predators. Nevertheless, other guilds are known, such as cecidophages, symbionts and kleptoparasites, but they were not been cited in these publications, probably due to terminological problems.

Mani (1964) defined most of these guilds. According to this author, successors are organisms that use the gall after the inducer leaves. They are mostly mites, spiders, thrips, beetles, ants and springtails, which apparently use gall tissues for food and shelter, but dead or decaying gall tissue is probably attacked by fungi that also serve as food. Inquilines and cecidophages use galls simultaneously with the galler. Both are phytophagous and consume gall tissues, but only the former promote the production of new tissues (they have been referred to as "gall modifiers" in some inventories). Kleptoparasites steal the resource (in this case the gall) from other organism, causing the galler death or its expulsion from the gall (Mound and Morris, 2000). Predators invade galls and feed on their inducers, killing them immediately, such as some species of Carabidae and Coccinellidae, for example (Ramamurthy, 2007). Parasitoids are organisms that live in close association with the host at the host's expense, which results in its death when the parasitoids complete their development (Godfray, 1994).

Guilds of predators, parasitoids, and successors are well delimited in the literature, while inquilines are a major problem as historically all organisms associated with galls that were not predators or parasitoids were placed in this guild (Redfern and Askew, 1992). Mani (1964), Godfray (1994), and Mound and Morris (2000) provided tools for distinguishing among these guilds, but none of them used multiple non-superposed parameters.

Luz and Mendonça-Júnior (2017) proposed five interaction parameters to conceptualize and differentiate inquilines, cecidophages and kleptoparasites from each other: food habit; coexistence with the inducer; modification of gall tissues or production of new tissues; phylogenetic relationship with the inducer; and mobility. According to these authors, inquilines are exclusively phytophagous, coexist with the gall-inducer, modify gall tissues or stimulate production of new tissues, have a close phylogenetic relationship with the inducer and are sedentary. Cecidophages are exclusively phytophagous, coexist with the gall-inducer, but do not modify gall tissues or stimulate production of new tissues, do not have a close phylogenetic relationship with the inducer and have high mobility, while kleptoparasites are omnivorous, do not coexist with the inducer, do not modify gall tissues or stimulate production of new tissues, can have a close phylogenetic relationship with the inducer and have low mobility. Based on these criteria, the inquilinous fauna associated with insect galls in Brazilian restingas is reviewed herein.

This paper also aims to answer the following questions: (1) Which are the most frequent and richest taxa of inquilines, cecidophages, and kleptoparasites? (2) Which gall-inducing taxa host the richest fauna of inquilines, cecidophages, and kleptoparasites? (3) In how many gall morphotypes and plant species, genera and families have these guilds been recorded? (4) Which plant families, genera and species shelter the richest guilds of inquilines, cecidophages, and kleptoparasites? (5) What are the most frequent features of host galls? (6) What is known about the taxonomy of the inquilines, cecidophages, and kleptoparasites of gall? and (7) What is necessary for the correct positioning of the associated fauna in the different guilds?

2. Material and Methods

A survey of scientific papers involving Brazilian restingas published from 1988 to 2019 was carried out by consulting the database "Web of Science" using "*gall*" or "*galha*" and "*restinga*" as keywords. Sixteen publications about galls in Brazilian restingas were found and examined. Eight of the publications provided data on inquilinous fauna, which were retrieved, compiled and analyzed, following the criteria established by Luz and Mendonça-Júnior (2017). The new positioning of associated fauna among guilds was based on literature data, as well as on unpublished biological information obtained from laboratory works, including gall arthropod rearing, gall dissection and observation of gall tissues and gall dweller behavior. These laboratory works were carried out during inventories of which I have participated, namely Maia, 2001; Maia et al., 2008; Bregonci et al., 2010; and Rodrigues et al. 2014. Finally, the positioning of the associated fauna into parasitoid and predator guilds was not revised, since the conceptions of these guilds are well understood.

3. Results

3.1. Literature data

Eight publications provided data on inquilinous fauna: Bregonci et al. (2010), Maia (1995, 2001, 2013), Maia and Azevedo (2009), Maia et al. (2002, 2008), and Rodrigues et al. (2014). However, this guild was misinterpreted, since it also comprised cecidophages and kleptoparasites, without discriminating them. Diptera (Cecidomyiidae, Chloropidae, Muscomorpha, Sciaridae, and Tephritidae), Coleoptera, Hemiptera (Aphidae, Coccidae, and Tingidae), Hymenoptera (Eulophidae, Formicidae and Tanaostigmatidae), Lepidoptera, and Thysanoptera were represented among the taxa indicated as inquilines by these authors (Table 1), with Diptera, Lepidoptera, and Coleoptera being the most frequent (Table 2). This secondary fauna was found in 53 gall morphotypes and totaled 65 records in 44 plant species and four morphospecies distributed among 36 genera of 24 host families. Myrtaceae was the family with the greatest number of records (Table 3). Most inquilines were positioned in other guilds, as shown below.

Table 1. Inquilines found in insect gall inventories in Brazilian restingas published from 1988 to 2019.

Host Plant		Gall-inducer	Inquiline	Reference
Family	**Species**			
Anacardiaceae	*Atronium* sp.	Hemiptera	*Clinodiplosis* sp. (Cecidomyiidae)	Maia (2013)
Asteraceae	*Mikania* cf. *biformis* DC.	*Mikaniadiplosis annulipes* Gagné, 2001 (Cecidomyiidae)	*Contarinia ubiquata* Gagné, 2001 (Cecidomyiidae)	Maia et al. (2008)
		Liodiplosis conica Gagné, 2001 (Cecidomyiidae)	*Trotteria* sp. (Cecidomyiidae)	Maia et al. (2008)
		Liodiplosis conica Gagné, 2001 (Cecidomyiidae)	*Acanthocheilla* sp. (Tingidae) Aphididae and Coccidae (Hemiptera), Curculionidae (Coleoptera),	
	Baccharis singularis (Vell.) G. M. Barroso	*Neolasioptera* sp.	Thysanoptera	Maia et al. (2008)
	Baccharis speciosa DC.	Alycaulini (Cecidomyiidae)	Lepidoptera	Maia et al. (2008)
	Piptocarpha cf. *cinerea* Baker	Cecidomyiidi (Cecidomyiidae)	Lepidoptera	Maia et al. (2008)
		Asphondylia sp.	Lepidoptera and Curculionidae (Coleoptera)	Maia et al. (2008)
	Porophyllum ruderale (Jack.) Cass.	*Asphondylia* sp.	*Trypanea* sp. (Diptera, Tephritidae)	Rodrigues et al. (2014)
Bignoniaceae	*Parabignonia unguiculata* (Vell.) A. H. Gentry	Cecidomyiidae	*Resseliella* sp. (Cecidomyiidae)	Maia et al. (2008)
Boraginaceae	*Varronia curassavica* Jacq.	Lopesiini (Cecidomyiidae)	Curculionidae (Coleoptera)	Maia et al. (2008)
Calophyllaceae	*Calophyllum brasiliense* Cambess.	*Lopesia elliptica* Maia, 2003 (Cecidomyiidae)	Coleoptera	Maia et al. (2008)
Celastraceae	*Elachyptera micrantha* (Cambess.) A. C. Sm.	Cecidomyiidae	Lepidoptera	Maia et al. (2008)
Erythroxylaceae	*Erythroxylum ovalifolium* Peyrs	*Lopesia erythroxyli* Rodrigues and Maia, 2010	Eulophidae (gall modifier)	Maia (2001
Euphorbiaceae	*Croton compressus* Lam.	Not determined	Curculionidae (Coleoptera)	Rodrigues et al. (2014)
Fabaceae	*Andira fraxinifolia* Benth.	*Lopesia indaiensis* Maia & Oliveira, 2018	Curculionidae (Coleoptera), Lepidoptera and Cecidomyiidae	Maia et al. (2008), Rodrigues et al. (2014)
		Asphondyliina	Curculionidae (Coleoptera)	Maia et al. (2008)
	Andira nitida Mart. ex Benth.	Cecidomyiidae	Coleoptera	Bregonci et al. (2010)
	Inga laurina (Sw.) Willd.	*Meunieriella* sp. (Cecidomyiidae, Diptera)	Tanaostigmatidae (Hymenoptera)	Maia et al. (2002)
	Inga sp.	*Neolasioptera* sp. (Cecidomyiidae)	Lepidoptera	Rodrigues et al. (2014)
Lamiaceae	*Hyptis fasciculata* Benth.	Cecidomyiidae	Curculionidae (Coleoptera)	Maia et al. (2008)
Lauraceae	*Ocotea lobbii* (Meisn.) Rohwer	Not determined	*Trotteria* sp. (Cecidomyiidae)	Maia et al. (2008)
	Ocotea notata (Nees & Mart.) Mez	Hemiptera	Cecidomyiidae	Bregonci et al. (2010)

Table 1. Continued...

Host Plant		Gall-inducer	Inquiline	Reference
Family	**Species**			
	Ocotea pulchella (Nees) Mez	Cecidomyiidae	Hemiptera	Maia et al. (2008)
		Not determined	*Trotteria* sp. (Cecidomyiidae)	Maia et al. (2008)
Loranthaceae	*Struthanthus concinnus* Mart.	*Asphondylia* sp. (Cecidomyiidae)	Cecidomyiidae and Thysanoptera	Rodrigues et al. (2014)
Malvaceae	*Luehea divaricata* Mart	Cecidomyiidae	*Olcella* sp. (Chloropidae, Diptera)	Rodrigues et al. (2014)
Melastomataceae	*Miconia cinnamomifolia* (DC.) Naudin.	*Epihormomyia miconiae* Maia, 2001 (Cecidomyiidae)	*Resseliella* sp. (Cecidomyiidae)	Maia (2001)
	Tibouchina trichopoda (DC.) Baill.	Cecidomyiidae	Curculionidae (Coleoptera)	Maia et al. (2008)
Myrtaceae	*Campomanesia guaviroba* (DC.) Kiaersk.	*Clinodiplosis* sp. (Cecidomyiidae)	Membracidae (Hemiptera)	Maia et al. (2008)
	Eugenia astringens Cambess.	*Stephomyia rotundifoliorum* Maia, 1994	Eulophidae (gall modifier)	Maia (2001)
	Eugenia copacabanensis Kiaersk.	*Stephomyia tetralobae* Maia, 1994	*Trotteria* sp. (Cecidomyiidae)	Maia (1995)
	Eugenia hiemalis Cambess.	*Stephomyia* sp.	*Leptothorax* sp. (Formicidae, Hymenoptera)	Maia (2001)
	Eugenia punicifolia (Kunt) DC.	Not determined	Curculionidae (Coleoptera)	Rodrigues et al. (2014)
	Eugenia speciosa Cambess.	Schizomyiina *Clinodiplosis* sp. (Cecidomyiidae)	Sciaridae (Diptera)	Maia et al. (2008)
	Myrcia ovata Cambess.	*Myrciamyia maricaensis* Maia, 1995 (Cecidomyiidae)	Eulophidae sp.1 (gall modifier), Eulophidae sp. 2 (endogaller)	Ferraz and Monteiro (2003)
	Myrciaria floribunda (H.West ex Willd.) O. Berg	Cecidomyiidae	Thysanoptera	Bregonci et al. (2010)
	Neomitranthes obscura (DC.) N. J. E. Silveira	*Neomitranthella robusta* Maia, 1996 (Cecidomyiidae)	*Stenoma annosa* (Butler, 1877) (Lepidoptera)	Personnal observation
		Cecidomyiidae	*S.annosa*	Maia (2001)
Nyctaginaceae	*Guapira opposita* (Vell.) Reitz	*Bruggmannia elongata* Maia & Couri, 1993 (Cecidomyiidae)	Lepidoptera	Maia et al. (2008)
		Bruggmannia sp. (Cecidomyiidae)	Aphididae (Hemiptera)	Rodrigues et al. (2014)
		Pisphondylia sp.	Lepidoptera	Rodrigues et al. (2014)
	Guapira pernambucensis (Casar.) Lundell	Cecidomyiidae	Lepidoptera	Bregonci et al. (2010)
Ochnaceae	*Ouratea cuspidata* (A.St.-Hil.) Engl.	*Contarinia* sp. (Cecidomyiidae)	Coleoptera	Bregonci et al. (2010)
Peraceae	*Chaetocarpus myrsinites* Baill.	Not determined	Lepidoptera	Bregonci et al. (2010)
Polygalaceae	*Securidaca* sp.	Cecidomyiidae	Muscomorpha (Diptera)	Rodrigues et al. (2014)

Table 1. Continued...

Host Plant		Gall-inducer	Inquiline	Reference
Family	**Species**			
Polygonaceae	*Coccoloba alnifolia* Casar	*Lopesia* sp.	Lepidoptera	Rodrigues et al. (2014)
Sapindaceae	*Paullinia weinmanniifolia* Mart.	*Paulliniamyia ampla* Maia, 2001 (Cecidomyiidae)	Eulophidae (endogaller)	Maia (2001)
	Paullinia sp.	*Neolasioptera* sp. (Cecidomyiidae)	Lepidoptera	Maia et al. (2008)
	Serjania communis Cambess.	*Clinodiplosis* sp. (Cecidomyiidae)	Sciaridae (Diptera)	Maia et al. (2008)
Sapotaceae	*Pouteria venosa* (Mart.) Baehni	*Lopesia singularis* Maia, 2001 (Cecidomyiidae)	Lepidoptera	Maia et al. (2008)
	Manilkara subsericea (Mart.) Dubard	Cecidomyiidi (Cecidomyiidae)	*Contarinia* sp. (Cecidomyiidae)	Maia (2001)
		Cecidomyiidae	Coleoptera	Bregonci et al. (2010)
	Pouteria caimito (Ruiz & Pav.) Radlk.	*Youngomyia pouteriae* Maia, 2001 (Cecidomyiidae)	*Trotteria quadridentata* Maia, 2001 (Cecidomyiidae)	Maia (2013)
	Sideroxylon obtusifolium (Roem. & Schult.) T. D. Penn.	*Bruggmannniella sideroxyli* Rodrigues & Maia, 2020	Cecidomyiidae	Rodrigues et al. (2014)
Solanaceae	*Aureliana fasciculata* (Vell.) Sendtn.	*Clinodiplosis* sp. (Cecidomyiidae)	Curculionidae (Coleoptera)	Maia et al. (2008)
Verbenaceae	*Stachytarpheta* sp.	*Schizomyia stachytarphetae* Barnes, 1932 (Cecidomyiidae)	*Haplothrips gowdeyi* (Franklin, 1908) (Thysanoptera, Phlaeothripidae)	Rodrigues et al. (2014)

3.2. Recategorization (Table 4)

3.2.1. Cecidophage guild

Although Coleoptera, Sciaridae, Tephritidae, Chloropidae, Muscomorpha, *Clinodiplosis* sp. (Cecidomyiidae), Hemiptera, Lepidoptera, and Thysanoptera were represented among the taxa considered inquilines, biological observations indicated these to be cecidophages since they feed on galls without modifying them or stimulating production of new tissues, coexisted with the inducer and had high mobility.

Other laboratory observations showed that immature stages of dipterans, coleopterans and lepidopterans occurred in galls, but not the adults, since they left galls immediately after their emergence. Different from these insects, adult hemipterans and thysanopterans were frequently observed in galls together with their eggs and nymphs. Pupal exuviae of coleopterans, lepidopterans, tephritids and chloropids were found in galls, while those of sciarids remained attached to gall openings, in the same way as cecidomyiid exuviae.

Field and laboratory observations showed that caterpillars, such as that of *Stenoma annosa*, for example, could be voracious, feeding and destroying several galls (Butler, 1877). Furthermore, their excrement is accumulated in the internal chamber(s). These disturbances can lead to the death of the gall-inducer, as previously reported (Maia, 2001).

Whenever larvae of coleopterans and lepidopterans were observed, the gall-inducer died, which did not happen when dipterans, hemipterans and thysanopterans were present.

The cecidophage guild was obtained from 39 gall morphotypes (75%) on plants of 20 families (83%), 28 genera (78%) and 35 species (83%) (Table 5). Asteraceae and Myrtaceae were the host families with the greatest number of records, with ten and six, respectively, which corresponded to about 21% and 13% of the total. However, in both families, the number of gall morphotypes (six) and plant species (five) that hosted cecidophages was nearly the same, corresponding to 15% and 14%, respectively. Fabaceae totaled five records (11%), three gall morphotypes (8%), and three plant species (8%), followed by Nyctaginaceae with four (9%), four (10%) and three (8%), respectively.

Mikania Wild. (Asteraceae), *Andira* Juss. (Fabaceae), and *Guapira* Aubl. (Nyctaginaceae) were the plant genera with the highest number of records of cecidophages, with four each (9%). *Mikania* cf. *biformis* DC., *Andira fraxinifolia* Benth. (Fabaceae), *Guapira opposita* (Vell.) Reitz (Nyctaginaceae), *Piptocarpha* cf. *cinerea* Baker, and *Neomitranthes obscura* (DC.) N. J. E. Silveira (Myrtaceae) were the plant species

Table 2. Number of host species, gall morphotypes and records of inquilines by plant family in insect gall inventories in Brazilian restingas published from 1988 to 2019.

Host Plant		Number of gall morphotypes	Number of records of inquilines
Family	Number of species		
Myrtaceae	9	10	11
Asteraceae	5	8	11
Fabaceae	4	5	7
Sapotaceae	4	5	5
Lauraceae	3	4	4
Nyctaginaceae	2	4	4
Sapindaceae	3	3	3
Melastomataceae	2	2	2
Anacardiaceae	1	1	1
Bignoniaceae	1	1	1
Boraginaceae	1	1	1
Calophyllaceae	1	1	1
Celastraceae	1	1	1
Erythroxylaceae	1	1	1
Euphorbiaceae	1	1	1
Lamiaceae	1	1	1
Loranthaceae	1	1	2
Malvaceae	1	1	1
Ochnaceae	1	1	1
Peraceae	1	1	1
Polygalaceae	1	1	1
Polygonaceae	1	1	1
Solanaceae	1	1	1
Verbenaceae	1	1	1

Table 3. Frequency of inquilines in insect gall inventories in Brazilian restingas published from 1988 to 2019.

Inquiline		Number of records
Diptera		19
	Cecidomyiidae	14
	Sciaridae	2
	Chloropidae	1
	Muscomorpha	1
	Tephritidae	1
Lepidoptera		15
Coleoptera		14
Hymenoptera		7
Thysanoptera		4
Hemiptera		6

with more than one cecidophage record. The first hosted aphidids, coccids, tingids (Hemiptera), and curculionids (Coleoptera) in only one gall morphotype; the second hosted curculionids and lepidopterans in one morphotype as well; the third hosted curculionids and lepidopterans in two morphotypes; and the last, hosted lepidopterans in two gall morphotypes.

Concerning plant organs, cecidophages were obtained from galls on leaves, stems, buds, tendrils, flowers, and fruits, with leaf galls being most frequent (61%). They occurred in galls of several shapes, but mainly in globoid galls (31%). Although they were obtained from green, brown, yellow, red, and purple galls, 67% occurred in green galls, and 95% occurred in glabrous galls.

Cecidophages represented five insect orders: Coleoptera, Diptera (Cecidomyiidae, Chloropidae, Muscomorpha, Sciaridae, Tephritidae), Hemiptera (Aphididae, Membracidae), Lepidoptera, and Thysanoptera. Among these, lepidopterans and coleopterans were the

Table 4. Records of cecidophages, kleptoparasites, and inquilines in insect galls in Brazilian restingas.

Host Plant	Gall-inducers	Associated fauna
Atronium sp.	Hemiptera	*Clinodiplosis* sp. (cecidophage)
Mikania cf. *biformis* DC.	*Mikaniadiplosis annulipes* Gagné, 2001	*Contarinia ubiquita* Gagné, 2001 (kleptoparasite)
	Liodiplosis conica Gagné. 2001	*Trotteria* sp. (kleptoparasite)
Baccharis singularis (Vell.) G. M. Barroso	*Neolasioptera* sp.	Thysanoptera (cecidophage)
Baccharis speciosa DC.	Alycaulini	Lepidoptera (cecidophage)
Piptocarpha cf. *cinerea* Baker	Cecidomyiidi	Lepidoptera (cecidophage)
Porophyllum ruderale (Jack.) Cass.	*Asphondylia* sp.	*Trypanea* sp. (cecidophage)
Parabignonia unguiculata (Vell.) A. H. Gentry	Cecidomyiidae	*Resseliella* sp. (kleptoparasite)
Varronia curassavica Jacq.	Lopesiini	Curculionidae (cecidophage)
Calophyllum brasiliense Cambess.	*Lopesia elliptica* Maia, 2003	Coleoptera (cecidophage)
Elachyptera micrantha (Cambess.) A. C. Sm.	Cecidomyiidae	Lepidoptera (cecidophage)
Erythroxylum ovalifolium Peyrs.	*Lopesia erythroxyli* Rodrigues and Maia, 2010	Eulophidae (inquiline)
Croton compressus Lam.	Not determined	Curculionidae (cecidophage)
Andira fraxinifolia Benth.	Cecidomyiidi	Curculionidae and Lepidoptera (cecidophages)
	Asphondyliina	Curculionidae (cecidophage)
	Lopesia indaiensis Maia & Oliveira, 2018	Cecidomyiidae (kleptoparasite)
	Cecidomyiidae	Coleoptera (cecidophage)
Inga laurina (Sw.) Willd.	*Meunieriella* sp.	Tanaostigmatidae (kleptoparasite)
Inga sp.	*Neolasioptera* sp.	Lepidoptera (cecidophage)
Hyptis fasciculata Benth.	Cecidomyiidae	Curculionidae (cecidophage)
Ocotea lobbii (Meisn.) Rohwer	Not determined	*Trotteria* sp. (kleptoparasite)
Ocotea notata (Nees & Mart.) Mez	Hemiptera	Cecidomyiidae (cecidophage)
Ocotea pulchella (Nees) Mez	Cecidomyiidae	Hemiptera (cecidophage)
	Not determined	*Trotteria* sp. (kleptoparasite)
Struthanthus concinnus Mart.	*Asphondylia* sp.	Cecidomyiidae (kleptoparasite) and Thysanoptera (cecidophage)
Luehea divaricata Mart.	Cecidomyiidae	*Olcella* sp. (cecidophage)
Miconia cinnamomifolia (DC.) Naudin.	*Epihormomyia miconiae* Maia, 2001	*Resseliella* sp. (kleptoparasite)
Tibouchina trichopoda (DC.) Baill.	Cecidomyiidae	Curculionidae (cecidophage)
Campomanesia guaviroba (DC.) Kiaersk.	*Clinodiplosis* sp.	Membracidae (cecidophage)
Eugenia astringens Cambess.	*Stephomyia rotundifoliorum* Maia, 1994	Eulophidae (inquiline)
Eugenia copacabanensis Kiaersk.	*Stephomyia tetralobae* Maia, 1994	*Trotteria* sp. (kleptoparasite)
Eugenia hiemalis Cambess.	*Stephomyia* sp.	*Leptothorax* sp. (successor)
Eugenia punicifolia (Kunt) DC.	Not determined	Curculionidae (cecidophage)
Eugenia speciosa Cambess.	Schizomyiina	Sciaridae (cecidophage)
Myrcia ovata Cambess.	*Myrciamyia maricaensis* Maia, 1995	Eulophidae sp.1 and Eulophidae sp. 2 (inquilines)
Myrciaria floribunda (H.West ex Willd.) O. Berg	Cecidomyiidae	Thysanoptera (cecidophage)
Neomitranthes obscura (DC.) N. J. E. Silveira	*Neomitranthella robusta* Maia, 2001	*Stenoma annosa* (Butler, 1877) (cecidophage)

Table 4. Continued...

Host Plant	Gall-inducers	Associated fauna
	Clinodiplosini	*Stenoma annosa* (cecidophage)
Guapira opposita (Vell.) Reitz	*Bruggmannia elongata* Maia & Couri, 1993	Lepidoptera (cecidophage)
	Bruggmannia sp.	Aphididae (cecidophage)
	Pisphondylia sp.	Lepidoptera (cecidophage)
G. pernambucensis (Casar.) Lundell	Cecidomyiidae	Lepidoptera (cecidophage)
Ouratea cuspidata (A.St.-Hil.) Engl.	*Contarinia* sp.	Coleoptera (cecidophage)
Chaetocarpus myrsinites Baill.	Not determined	Lepidoptera (cecidophage)
Securidaca sp.	Cecidomyiidae	Muscomorpha (cecidophage)
Coccoloba alnifolia Casar	*Lopesia* sp.	Lepidoptera (cecidophage)
Paullinia weinmanniifolia Mart.	*Paulliniamyia ampla* Maia, 2001	Eulophidae (inquiline)
Paullinia sp.	*Neolasioptera* sp. (Cecidomyiidae)	Lepidoptera (cecidophage)
Serjania communis Cambess.	*Clinodiplosis* sp.	Sciaridae (cecidophage)
Pouteria venosa (Mart.) Baehni	*Lopesia singularis* Maia, 2001	Lepidoptera (cecidophage)
Manilkara subsericea	Cecidomyiidi	*Contarinia* sp. (kleptoparasite)
(Mart.) Dubard	Cecidomyiidae	Coleoptera (cecidophage)
Pouteria caimito (Ruiz & Pav.) Radlk.	*Youngomyia pouteriae* Maia, 2001	*Trotteria quadridentata* Maia, 2001 (kleptoparasite)
Sideroxylon obtusifolium (Roem. & Schult.) T. D.	*Bruggmannniella sideroxyli* Rodrigues & Maia, 2020	Cecidomyiidae (kleptoparasite)
Aureliana fasciculata (Vell.) Sendtn.	*Clinodiplosis* sp.	Curculionidae (cecidophage)
Stachytarpheta sp.	*Schizomyia stachytarphetae* Barnes, 1932	*Haplothrips gowdeyi* (Franklin, 1908) (cecidophage)

Table 5. Cecidophages, kleptoparasites and inquilines found in gall inventories in Brazilian restingas and gall characterization.

Guilds	Host plant	Gall characterization			
Inquilines		**Host organ**	**Shape**	**Color**	**Trichomes**
Eulophidae	*Erythroxylum ovalifolium* Peyrs.	Bud	Conical	Green	Absent
Eulophidae	*Eugenia astringens* Cambess.	Bud	Cylindrical	Brown	Absent
Eulophidae sp.1	*Myrcia ovata* Cambess.	Bud	Ovoid	Green	Absent
Eulophidae sp. 2	*Myrcia ovata*	Bud	Ovoid	Green	Absent
Eulophidae	*Paullinia weinmanniifolia* Mart.	Leaf	Conical	Green	Absent
Kleptoparasites					
Cecidomyiidae	*Andira fraxinifolia* Benth.	Leaf	Vermiform	Green	Absent
Cecidomyiidae	*Struthanthus concinnus* Mart.	Leaf and stem	Conical	Green	Absent
Cecidomyiidae	*Sideroxylon obtusifolium* (Roem. & Schult.) T. D. Penn.	Fruit	Globoid	Green	Absent
Contarinia ubiquita	*Mikania* cf. *biformis* DC.	Leaf vein, petiole and stem	Fusiform	Green	Absent
Contarinia sp.	*Manilkara subsericea* (Mart.) Dubard	Leaf	Lenticular	Green	Absent
Resseliella sp.	*Parabignonia unguiculata* (Vell.) A. H. Gentry	Leaf	Lenticular	Green	Absent
Resseliella sp.	*Miconia cinnamomifolia* (DC.) Naudin.	Bud	Ovoid	Green	Absent

Table 5. Continued...

Guilds	Host plant	Gall characterization			
Inquilines		**Host organ**	**Shape**	**Color**	**Trichomes**
Tanaostigmatidae	*Inga laurina* (Sw.) Willd.	Leaf	Cylindrical	Yellow	Absent
Trotteria quadridentata	*Pouteria caimito* (Ruiz & Pav.) Radlk.	Leaf	Conical	Green	Absent
Trotteria sp.	*Mikania* cf. *biformis* DC.	Leaf and stem	Conical	Green	Absent
Trotteria sp.	*Ocotea lobbii* (Meisn.) Rohwer	Stem	Fusiform	Brown	Absent
Trotteria sp.	*Ocotea pulchella* (Nees) Mez	Stem	No data	No data	No data
Trotteria sp.	*Eugenia copacabanensis* Kiaersk.	Leaf	Fusiform	Red	Absent
Cecidophages					
Clinodiplosis sp.	*Atronium* sp.	Leaf	Globoid	Green	Absent
Thysanoptera	*Baccharis singularis* (Vell.) G. M. Barroso	Leaf and stem	No data	No data	No data
Acanthocheilla sp. (Tingidae, Hemiptera)	*Mikania* cf. *biformis* DC.	Leaf	Globoid	Green	Absent
Aphididae (Hemiptera)	*Mikania* cf. *biformis*	Leaf	Globoid	Green	Absent
Coccidae (Hemiptera)	*Mikania* cf. *biformis*	Leaf	Globoid	Green	Absent
Curculionidae (Coleoptera)	*Mikania* cf. *biformis*	Leaf	Globoid	Green	Absent
Lepidoptera	*Baccharis speciosa* DC.	Stem and bud	No data	No data	No data
Lepidoptera	*Piptocarpha* cf. *cinerea* Baker	Leaf vein, stem and bud	Ovoid	Brown	Absent
Curculionidae (Coleoptera)	*Piptocarpha* cf. *cinerea*	Leaf petiole, stem, bud	Globoid	Brown	Absent
Lepidoptera	*Piptocarpha* cf. *cinerea*	Leaf petiole, stem, bud	Globoid	Brown	Absent
Trypanea sp.	*Porophyllum ruderale* (Jack.) Cass.	Inflorescence	Fusiform	Green	Absent
Curculionidae	*Varronia curassavica* Jacq.	Leaf vein	Fusiform	Green	Absent
Coleoptera	*Calophyllum brasiliense* Cambess.	Leaf	Fusiform	Green	Absent
Lepidoptera	*Elachyptera micranta* (Cambess.) A. C. Sm.	Leaf and bud	Conical	Green	Absent
Curculionidae	*Croton compressus* Lam.	Inflorescence	Amorphous	Yellow	Present
Curculionidae	*Andira fraxinifolia* Benth.	Leaf	Vermiform	Green	Absent
Lepidoptera	*Andira fraxinifolia*	Leaf	Vermiform	Green	Absent
Curculionidae	*Andira fraxinifolia*	Leaf	Vermiform	Green	Absent
Coleoptera	*Andira nitida* Mart. ex Benth	Leaf	Lenticular	Green	Absent
Lepidoptera	*Inga* sp.	Stem	Fusiform	Green, Brown	Present
Curculionidae	*Hyptis fasciculata* Benth.	Leaf vein, petiole and stem	Fusiform	Green brown	Absent
Cecidomyiidae	*Ocotea notata* (Nees & Mart.) Mez	Leaf	Lenticular	Green yellow	Absent
Hemiptera	*Ocotea pulchella* (Nees) Mez	Stem and bud	Fusiform	No data	Absent
Thysanoptera	*Struthanthus concinnus* Mart.	Leaf and stem	Conical	Green	Absent
Olcella sp.	*Luehea divaricata* Mart.	Stem	Globoid	Brown	Absent
Curculionidae	*Tibouchina trichopoda* (DC.) Baill.	Stem	Fusiform	Brown	Absent
Membracidae	*Campomanesia guaviroba* (DC.) Kiaersk.	Leaf vein	Globoid	No data	Absent

Table 5. Continued...

Guilds	Host plant	Gall characterization			
Inquilines		**Host organ**	**Shape**	**Color**	**Trichomes**
Curculionidae	*Eugenia punicifolia* (Kunt) DC.	Fruit	Globoid	Green, yellow, Red	Absent
Sciaridae	*Eugenia speciosa* Cambess.	Leaf	Conical	Yellow	Absent
Thysanoptera	*Myrciaria floribunda* (H.West ex Willd.) O. Berg	Leaf	Globoid	Green	Present
Stenoma annosa	*Neomitranthes obscura* (DC.) N. J. E. Silveira	Leaf	Marginal roll	Green	Absent
S.annosa	*Neomitranthes obscura*	Bud	Conical	Green	Absent
Lepidoptera	*Guapira opposita* (Vell.) Reitz	Leaf	Lenticular	Green	Absent
Aphididae	*Guapira opposita*	Leaf	Globoid	Brown	Absent
Lepidoptera	*Guapira opposita*	Flower peduncle	Globoid	Green, Brown, red	Absent
Lepidoptera	*Guapira pernambucensis* (Casar.) Lundell	Leaf	Lenticular	Green	Absent
Coleoptera	*Ouratea cuspidata* (A.St.-Hil.) Engl.	Leaf	Conical	Brown	Absent
Lepidoptera	*Chaetocarpus myrsinites* Baill.	Leaf	Lenticular	Green, Brown	Absent
Muscomorpha	*Securidaca* sp.	Closed flower	Ovoid	Purple	Absent
Lepidoptera	*Coccoloba alnifolia* Casar	Inflorescence	Globoid	Green, Yellow	Absent
Lepidoptera	*Paullinia* sp.	Leaf petiole, vein and tendril	Fusiform	Green	Absent
Sciaridae	*Serjania communis* Cambess.	Bud	Ovoid	Red	Absent
Lepidoptera	*Pouteria venosa* (Mart.) Baehni	Leaf	Globoid	Green	Absent
Coleoptera	*Manilkara subsericea* (Mart.) Dubard	Leaf	Lenticular	Green	Absent
Curculionidae	*Aureliana fasciculata* (Vell.) Sendtn.	Leaf vein	Fusiform	Green	Absent
Haplothrips gowdeyi	*Stachytarpheta* sp.	Inflorescence	Globoid	Green	Present

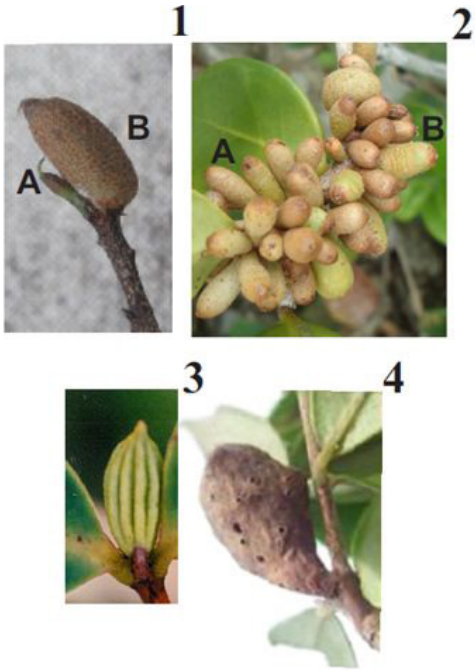
most frequent, being recorded in 38% and 36% of the galls with cecidophagous insects, while dipterans, hemipterans, and thysanopterans were recorded in 15%, 13%, and 13% of the galls, respectively.

Only two cecidophages were identified to species: *Stenoma annosa* (Lepidoptera) and *Haplothrips gowdeyi* (Thysanoptera). Four were identified to genus: *Clinodiplosis* (Cecidomyiidae), *Acanthocheilla* (Tingidae), *Trypanea* (Tephritidae), and *Olcella* (Chloropidae). All other cecidophage records were identified to suprageneric categories.

3.2.2. Inquiline guild

Only eulophids (Hymenoptera) were considered inquilines in this revision, since their larvae were sedentary, exclusively phytophagous, coexisted with the gall-inducer and caused modification of gall tissues or stimulated the production of new tissues.

Modifications of gall tissues were reported in three gall morphotypes, one induced by *Lopesia erythroxyli* Rodrigues & Maia, 2010 (Cecidomyiidae) on *Erythroxylum ovalifolium* Peyrs (Erythoxylaceae) (Figure 1), another induced by *Stephomyia rotundifoliorum* Maia, 1994 (Cecidomyiidae) on *Eugenia astringens* Camb. (Myrtaceae) (Figure 2), and the third induced by *Myrciamyia maricaensis* Maia, 1995 (Cecidomyiidae) on *Myrcia ovata* Camb. (Myrtaceae). The production of new tissues was reported in two gall morphotypes, one induced by *Paulliniamyia ampla* Maia, 2001 (Cecidomyiidae) on *Paullinia weinmanniifolia* Mart. (Sapindaceae) and the other induced by *M. maricaensis* on *Myrcia ovata* (Figures 3 and 4). None of these inquilines



Figures 1-4. Galls of Cecidomyiidae. 1. Galls on *Erythroxylum ovalifolium* Peyrs. (Erythroxylaceae): (A) Gall induced by *Lopesia erythroxyli* Rodrigues and Maia, 2010; (B) The same gall modified by Eulophidae (Hymenoptera). 2. Galls on *Eugenia astringens* Cambess. (Myrtaceae): (A) Gall induced by *Stephomyia rotundifoliorum* Maia, 1994; (B) The same gall modified by Eulophidae (Hymenoptera). 3-4. Galls on *Myrcia ovata* Cambess. (Myrtaceae): 3. Gall induced by *Myrciamyia maricaensis* Maia, 1995, 4. The same gall modified by Eulophidae sp. 2 (Hymenoptera).

had a close phylogenetic relationship with the gall-inducer, and whenever they were present, the gall-inducers died.

Collectively, inquilines totaled five records (less than 8%) in four gall morphotypes (less than 8%) on plants of three families (16%), four genera (11%) and four species (9%), all with a similar number of records (Table 5).

Inquilines were found mainly in bud galls, but also in leaf galls. They occurred in conical, ovoid, and cylindrical galls, with the first two being more frequent. They were obtained mainly from green galls, but also from brown galls, and all occurred in glabrous galls. Inquilines were identified only to the family level.

3.2.3. Sucessors

Leptothorax sp. (Formicidae) was reported as an inquiline of cylindrical galls on *Eugenia hiemalis* Camb. (Myrtaceae) by Maia (2001), but no gall modification was related to the presence of this ant. Furthermore, *Leptothorax* sp. could not be considered cecidophagous since it did not feed on gall tissues. Maia (2001) reported *Leptothorax* sp. as a successor in similar galls on *Eugenia astringens* Cambess. (Myrtaceae). These two cases are probably the same.

3.2.4. Kleptoparasites

Larvae of species of *Contarinia*, *Resseliella*, and *Trotteria* (Cecidomyiidae) were recorded in galls of other cecidomyiids, indicating a close phylogenetic relationship with the inducer since all belong to the same family. Whenever they were observed, they were the unique dwellers of galls, so the criterion of non-coexistence was fulfilled. Furthermore, these larvae showed low mobility and did not modify or stimulate production of new gall tissues. Therefore, they can be considered as kleptoparasites. Nevertheless, the criterion of food habit was not met, since their larvae were phytophagous and not omnivorous.

Tanaostigmatids, reported in galls of *Meunieriella* (Cecidomyiidae), were also considered kleptoparasites.

This guild totaled 13 records (20%) in 12 gall morphotypes (23%) on plants of eight families (33%), 11 genera (30%) and 12 species (27%). All plant taxa had a similar number of records, so none of them can be highlighted as the most frequent (Table 5).

Kleptoparasites were represented by cecidomyiids (Diptera) and tanaostigmatids (Hymenoptera), which were obtained from leaf, stem, bud and fruit galls, being more frequent in the leaf galls (69%). Kleptoparasites occurred in conical, globoid, fusiform, lenticular, ovoid, cylindrical and vermiform galls, but mainly in the first (33%). Galls were green, yellow, brown, and red, but most (75%) were green. All reports were in glabrous galls.

Two kleptoparasites were identified to species, *Contarinia ubiquita* and *Trotteria quadridentata* (Cecidomyiidae), seven to genera, *Contarinia* (N=1), *Resseliella* (N=2), and *Trotteria* (N=4), and four to family, Cecidomyiidae (N=3) and Tanaostigmatidae (N=1).

3.3. Gall-inducing taxa and cecidophage, inquiline and kleptoparasite guilds

Cecidophages, inquilines and kleptoparasites were recorded in 46 gall morphotypes induced by cecidomyiids (Diptera) and in two morphotypes induced by hemipterans. Cecidomyiid galls comprised all three of these guilds, while those of hemipterans sheltered only cecidophages. Some kleptoparasites and cecidophages were obtained from five gall morphotypes (9% of the total) whose inducers are still unknown.

Cecidophages, inquilines and kleptoparasites were associated with 16 species and 15 morphospecies of gall-inducing cecidomyiids of 18 genera. Among these, galls induced by species of *Lopesia* Rübsaamen, 1908, hosted the greatest variety of guilds (cecidophages, inquilines, and kleptoparasites) and associated taxa (Coleoptera, Eulophidae, Cecidomyiidae, and Lepidoptera), followed by galls induced by species of *Stephomyia* Tavares, 1916, the galls of which sheltered inquilines (Eulophidae) and kleptoparasites (*Trotteria* sp.). Galls induced by species of *Clinodiplosis* Kieffer, 1894, hosted only cecidophages, as did those induced by species of *Neolasioptera* Felt, 1908, *Asphondylia* Loew, 1850, and *Bruggmannia* Tavares, 1906. Membracids, sciarids and curculionids were recorded in galls of *Clinodiplosis*, while thysanopterans and lepidopterans were recorded in galls of *Neolasioptera*. Representatives of Diptera (Cecidomyiidae and *Trypanea* sp.: Tephritidae) and Thysanoptera were obtained from galls of *Asphondylia*,

whereas representatives of Hemiptera (Aphididae) and Lepidoptera were obtained from galls of *Bruggmannia*. The other gall midge genera sheltered a single guild and a single insect taxon.

Gall-inducing hemipterans were identified only to the level of order. Their galls hosted cecidomyiids, one of them identified to genus (*Clinodiplosis* sp.) and the other to family.

The new composition of these guilds allows the questions proposed at the beginning of this paper to be answered:

1) The most represented taxa among cecidophages were Lepidoptera and Coleoptera. Inquilines represented only Eulophidae (Hymenoptera) and kleptoparasites mainly Cecidomyiidae (Diptera). The richest taxa were not indicated, as most records were in suprageneric categories, without the discrimination of morphospecies;
2) Cecidomyiidae is the gall-inducing taxon with the richest fauna of inquilines, cecidophages and kleptoparasites;
3) Inquilines were reported in four gall morphotypes, four plant species, four genera and three families; cecidophages in 39 gall morphotypes, 35 plant species, 28 genera, and 20 families; and kleptoparasites in 12 gall morphotypes, eight plant families, 11 genera, and 12 species;
4) Asteraceae and Myrtaceae, *Mikania* (Asteraceae), *Andira* (Fabaceae), and *Guapira* (Nyctaginaceae), *Mikania cf. biformis*, *Andira fraxinifolia* (Fabaceae), *Guapira opposita* (Nyctaginaceae), *Piptocarpha* cf. *cinerea*, and *Neomitranthes obscura* (Myrtaceae) were the plant taxa with the richest cecidophage guild. No plant taxa were highlighted as sheltering the richest kleptoparasite guild or inquiline guild;
5) Cecidophages, inquilines and kleptoparasites were recorded mainly in leaf, green, and glabrous galls. The first occurred more frequently in globoid galls, the second in conical and ovoid galls, and the last in conical galls;
6) The taxonomic knowledge of these guilds remains poor, since most were identified to suprageneric categories, and only four to species level;
7) Biological data are necessary for the correct positioning of associated fauna into guilds.

4. Discussion

In this review, the cecidophage guild was easily determined based on the five criteria proposed by Luz and Mendonça-Júnior (2017). On the other hand, some conceptual problems were faced in determining inquilines and kleptoparasites. According to these authors, inquilines have a close phylogenetic relationship with the gall-inducing species. This criterion was not met, but the other four (food habit, coexistence with the inducer, modification of gall tissues or production of new tissues, and mobility) were fulfilled. Regarding food habits, kleptoparasites are defined as omnivorous, which is a criterion not met by gall midges, although they met the other criteria. The use of these five criteria is only possible when biological data are known, which demands long-term studies.

The presence of cecidophages, inquilines and kleptoparasites can indirectly cause the death of the inducer, which can be important for population dynamics of gall-inducing species. However, this effect was little discussed in Luz and Mendonça-Júnior (2017). Nevertheless, these guilds should be considered since their presence can be an important mortality factor, as indicated by Maia, 2001.

Cecidophages were represented mainly by lepidopterans and coleopterans. These two insect orders were also indicated as the most represented among the secondary fauna inhabiting galls of cynipids (Hymenoptera) (Giannetti et al., 2019).

Cecidophage and kleptoparasite guilds were obtained mainly from leaf, green, and glabrous galls. These are the predominant features of insect galls in Brazilian restingas (Maia, 2001; Maia et al., 2008; Rodrigues et al., 2014), suggesting that guild frequency is related to resource availability. Nevertheless, other gall features were predominant for inquilines, but the number of records was too low to make generalizations. Most records were for cecidomyiid galls, the most diverse, abundant and frequent gall-inducing taxon in restingas (Maia, 2001; Maia et al., 2008; Rodrigues et al., 2014).

Asteraceae and Myrtaceae hosted the greatest richness and frequency of cecidophages, which was expected since they are the plant families with the greatest gall richness in restingas (Maia, 2013). Both families are well represented in this ecosystem (Lourenço and Barbosa, 2012; Melo-Júnior and Boeger, 2018). No plant family stood out as exhibiting the greatest number of kleptoparasite or inquiline records since both guilds were similarly distributed among different families. However, their records are also few, so new and broad studies are likely to modify this scenario.

The plant genera and species with the highest number of cecidophages were not necessarily those that hosted the greatest number of galls, since only *Mikania* and *Guapira opposita* (Nyctaginaceae) have been been cited as super host taxa (Maia and Oliveira, 2010; Maia, 2013; Rodrigues et al., 2014). Thus, cecidophage richness appears not to be related to gall richness. In fact, some galls can be more attractive than others, probably due to their own morphological and chemical features.

The high frequency of cecidophagy found here reveals the importance of gall-inducing insects as ecosystem engineers in restingas. Inducers do not merely provide habitat for specialists, but can also influence the structure of communities that do not directly interact with galls, as Wetzel et al. (2016) has shown. They can have significant impacts on the herbivore community not only by changing plant morphology, but also by altering host quality and modifying plant-induced responses to subsequent herbivory (Uesugi et al., 2016).

The taxonomic knowledge of cecidophage, kleptoparasite, and inquiline guilds remains still poor. The scarcity of identified species, for example, does not allow discussions to be made about their specificity.

A more complete review of guild richness, including also parasitoids, predators and symbionts, can contribute

to revealing the importance of associated faunas for gall systems. However, in order to know the composition of each guild, specific identification is essential, as well as the correct categorization of inquilines, kleptoparasites and cecidophages, which depends on taxonomical and biological data, respectively.

5. Conclusions

Although cecidophages were not previously recorded in insect gall inventories in Brazilian restingas, they are actually frequent. Kleptoparasites are also present. Both of these guilds are formally reported here for the first time in this ecosystem. On the other hand, the frequency and diversity of inquilines are low, differing from literature data. These new records resulted from recategorization among guilds based on literature data and biological observations, following criteria proposed by Luz and Mendonça-Júnior (2017).

Although the kleptoparasites found did not fulfill the food habit criterion, and the inquilines did not satisfy the phylogenetic relationship criterion, both guilds could be easily established based on the other four criteria. In my opinion, future studies about insect galls and associated fauna should adopt these criteria to avoid misinterpretation and improve knowledge about these guilds in Brazil.

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References

ANSALONI, S., SALMAZO, J.R. and URSO-GUIMARÃES, M.V., 2018. Entomogen galls in a Seasonal Semideciduous Forest area in Sorocaba, Southeast of São Paulo State, Brazil. *Biota Neotropica*, vol. 18, no. 4, pp. e20180523. http://dx.doi.org/10.1590/1676-0611-bn-2018-0523.

ARAÚJO, W.S., GOMES-KLEIN, V.L. and SANTOS, B.B., 2007. Galhas entomógenas associadas à vegetação do Parque Estadual da Serra dos Pireneus, Pirenópolis, Goiás, Brasil. *Revista Brasileira de Biociências*, vol. 5, suppl. 1, pp. 45-47.

ARAÚJO, W.S., SANTOS, B.B. and GOMES-KLEIN, V.L., 2011. Insect galls from Serra dos Pirineus, GO, Brazil. *Biota Neotropica*, vol. 11, no. 2, pp. 357-365. http://dx.doi.org/10.1590/S1676-06032011000200034.

ASCENDINO, S. and MAIA, V.C., 2018. Insects galls of Pantanal areas in the State of Mato Grosso do Sul, Brazil: characterization and occurrence. *Anais da Academia Brasileira de Ciências*, vol. 90, no. 2, pp. 1543-1564. http://dx.doi.org/10.1590/0001-3765201820170535. PMid:29791563.

BERGAMINI, B.A.R., BERGAMINI, L.L., SANTOS, B.B. and ARAÚJO, W.S., 2017. Occurrence and characterization of insect galls in the Floresta Nacional de Silvania. *Papéis Avulsos de Zoologia*, vol. 57, no. 32, pp. 413-431. http://dx.doi.org/10.11606/0031-1049.2017.57.32.

BREGONCI, J.M., POLYCARPO, P.V. and MAIA, V.C., 2010. Galhas de insetos do Parque Estadual Paulo César Vinha (Guarapari, ES, Brasil). *Biota Neotropica*, vol. 10, no. 1, pp. 265-274. http://dx.doi.org/10.1590/S1676-06032010000100023.

BRITO, G.P., COSTA, E.C., CARVALHO-FERNANDES, S.P. and SANTOS-SILVA, J., 2018. Riqueza de galhas de insetos em áreas de Caatinga com diferentes graus de antropização do estado da Bahia, Brasil. *Iheringia. Série Zoologia*, vol. 108, e2018003. http://dx.doi.org/10.1590/1678-4766e2018003.

CARVALHO, A.N. and MOTTA, J.S., 2018. Ocorrência e caracterização de galhas entomógenas em um fragmento florestal em estágio de sucessão ecológica na Amazônia. *EntomoBrasilis*, vol. 11, no. 2, pp. 118-123. http://dx.doi.org/10.12741/ebrasilis.v11i2.786.

CARVALHO-FERNANDES, S.P., ALMEIDA-CORTEZ, J. and FERREIRA, A.L.N., 2012. Riqueza de galhas entomógenas em áreas antropizadas e preservadas de caatinga. *Revista Árvore*, vol. 36, no. 2, pp. 269-277. http://dx.doi.org/10.1590/S0100-67622012000200008.

CARVALHO-FERNANDES, S.P., ASCENDINO, S., MAIA, V.C. and COURI, M.S., 2016. Diversity of insect galls associated with coastal shrub vegetation in Rio de Janeiro, Brazil. *Anais da Academia Brasileira de Ciências*, vol. 88, no. 3, pp. 1407-1418. http://dx.doi.org/10.1590/0001-3765201620150658. PMid:27627066.

COSTA, E.C., CARVALHO-FERNANDES, S.P. and SANTOS-SILVA, J., 2014. Galhas entomógenas associadas à Leguminosae do entorno do riacho Jatobá, Caetité, Bahia, Brasil. *Revista Brasileira de Biociências*, vol. 12, no. 2, pp. 115-120.

FERNANDES, G.W.A., TAMEIRÃO NETO, E. and MARTINS, R.P., 1988. Ocorrência e caracterização de galhas entomógenas do Campus Pampulha da Universidade Federal de Minas Gerais. *Revista Brasileira de Zoologia*, vol. 5, no. 1, pp. 11-29. http://dx.doi.org/10.1590/S0101-81751988000100002.

FERRAZ, F.F.F. and MONTEIRO, R.F., 2003. Complex interactions envolving a gall midge *Myrciamyia maricaensis* Maia (Diptera, Cecidomyiidae), phytophagous modifiers and parasitoids. *Revista Brasileira de Zoologia*, vol. 20, no. 3, pp. 433-437. http://dx.doi.org/10.1590/S0101-81752003000300011.

FLOR, I.C., FLOR, J.C.R. and FURTADO, P.S.N., 2018. Insect galls of the Floresta da Cicuta (Volta Redonda, RJ, Brazil). *Papéis Avulsos de Zoologia*, vol. 58, e20185824.

GIANNETTI, D., CASTRACANI, C., SPOTTI, F.A., MORI, A. and GRASSO, A., 2019. Gall-colonizing ants and their role as plant defenders: from "bad job" to "useful service". *Insects*, vol. 10, no. 11, pp. 392. http://dx.doi.org/10.3390/insects10110392. PMid:31698832.

GODFRAY, H.C.J., 1994. *Parasitoids: behavioral and evolutionary ecology*. Princeton: Princeton University Press, 473 p. http://dx.doi.org/10.1515/9780691207025.

LIMA, V.P. and CALADO, D., 2018. Morphological characterization of insect galls and new records of associated invertebrates in a Cerrado area in Bahia State, Brazil. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, vol. 78, no. 4, pp. 636-643. http://dx.doi.org/10.1590/1519-6984.169502. PMid:29319753.

LOURENÇO, A.R. and BARBOSA, M.R.V., 2012. Myrtaceae em restingas no limite norte de distribuição da Mata Atlântica, Brasil. *Rodriguésia*, vol. 63, no. 2, pp. 373-393. http://dx.doi.org/10.1590/S2175-78602012000200011.

LUZ, F.A. and MENDONÇA-JÚNIOR, M.S., 2017. Guilds in insect galls: who is who. *The Florida Entomologist*, vol. 102, no. 1, pp. 207-210. http://dx.doi.org/10.1653/024.102.0133.

MAIA, V.C. and CARVALHO-FERNANDES, S.P., 2016. Insect galls of a protected remnant of the Atlantic Forest tableland from Rio de Janeiro State (Brazil). *Revista Brasileira de Entomologia*, vol. 60, no. 1, pp. 40-56. http://dx.doi.org/10.1016/j.rbe.2015.09.001.

MAIA, V.C. and FERNANDES, G.W., 2004. Insect galls from Serra de São José (Tiradentes, MG, Brazil). *Brazilian Journal of Biology = Revista Brasileira de Biologia*, vol. 64, no. 3A, pp. 423-445. http://dx.doi.org/10.1590/S1519-69842004000300007. PMid:15622841.

MAIA, V.C. and MASCARENHAS, B., 2017. Insect galls of the Parque Nacional do Itatiaia (Southeast Region, Brazil). *Anais da Academia Brasileira de Ciências*, vol. 89, no. 1, suppl., pp. 505-575. http://dx.doi.org/10.1590/0001-3765201720160877. PMid:28562824.

MAIA, V.C. and OLIVEIRA, J.C., 2010. Galhas de insetos da Reserva Biológica Estadual da Praia do Sul (Ilha Grande, Angra dos Reis, RJ). *Biota Neotropica*, vol. 10, no. 4, pp. 227-238. http://dx.doi.org/10.1590/S1676-06032010000400028.

MAIA, V.C. and SIQUEIRA, E.S., 2020. Insect galls of the Reserva Biológica União, Rio de Janeiro, Brazil. *Biota Neotropica*, vol. 20, no. 1, pp. e20190758. http://dx.doi.org/10.1590/1676-0611-bn-2019-0758.

MAIA, V.C. and SOUZA, M.C., 2013. Insect galls of the xeric vegetation of Ilha do Cabo Frio (Arraial do Cabo, RJ, Brazil). *Biota Neotropica*, vol. 13, no. 3, pp. 278-288. http://dx.doi.org/10.1590/S1676-06032013000300030.

MAIA, V.C., 1995. Chaves para classificação de galhas de Cecidomyiidae (Diptera) em Myrtaceae na restinga da Barra de Maricá, Rio de Janeiro. *Revista Brasileira de Zoologia*, vol. 12, no. 4, pp. 1009-1013. http://dx.doi.org/10.1590/S0101-81751995000400028.

MAIA, V.C., 2001. The gall midges (Diptera, Cecidomyiidae) from three restingas of Rio de Janeiro State, Brazil. *Revista Brasileira de Zoologia*, vol. 18, no. 2, pp. 583-629. http://dx.doi.org/10.1590/S0101-81752001000200028.

MAIA, V.C., 2011. Characterization of insect galls, gall makers, and associated fauna of Platô Bacaba (Porto de Trombetas, Pará, Brazil). *Biota Neotropica*, vol. 11, no. 4, pp. 37-53. http://dx.doi.org/10.1590/S1676-06032011000400003.

MAIA, V.C., 2013. Insect galls of São Tomé das Letras (MG, Brazil). *Biota Neotropica*, vol. 13, no. 4, pp. 164-189. http://dx.doi.org/10.1590/S1676-06032013000400017.

MAIA, V.C., 2014. Insect galls of Itamonte (Minas Gerais, Brazil): characterization and occurrence. *Biota Neotropica*, vol. 14, no. 1, pp. 1-17. http://dx.doi.org/10.1590/S1676-06033839.

MAIA, V.C., AZEVEDO, M.A.P. and COURI, M.S., 2002. New contribution to the knowledge of the gall midges (Diptera, Cecidomyiidae) from the restinga of Barra de Maricá (Rio de Janeiro, Brazil). *Studia Dipterologica*, vol. 9, pp. 447-452.

MAIA, V.C. and AZEVEDO, M.A.P., 2009. Micro-himenópteros associados com galhas de Cecidomyiidae (Diptera) em restingas do estado do Rio de Janeiro. *Biota Neotropica*, vol. 9, no. 2, pp. 151-164. http://dx.doi.org/10.1590/S1676-06032009000200015.

MAIA, V.C., CARDOSO, J.L.T. and BRAGA, J.M.A., 2014. Insect galls from Atlantic Forest areas of Santa Teresa, Espírito Santo, Brazil: characterization and occurrence. *Boletim do Museu de Biologia Mello Leitão*, vol. 33, pp. 47-129.

MAIA, V.C., MAGENTA, M.A.G. and MARTINS, S.E., 2008. Ocorrência e caracterização de galhas de insetos em áreas de restinga de Bertioga (São Paulo, Brasil). *Biota Neotropica*, vol. 8, no. 1, pp. 167-197. http://dx.doi.org/10.1590/S1676-06032008000100020.

MANI, M.S., 1964. *Ecology of plant galls*. The Hague: Dr. W. Junk. http://dx.doi.org/10.1007/978-94-017-6230-4.

MELO-JÚNIOR, J.C.F. and BOEGER, M.R.T., 2018. Riqueza e estrutura de uma comunidade vegetal de dunas na planície costeira de Santa Catarina. *Iheringia. Série Botânica*, vol. 73, no. 3, pp. 290-297. http://dx.doi.org/10.21826/2446-8231201873306.

MOUND, L.A. and MORRIS, D.C., 2000. Inquilines or kleptoparasites? New phlaeothripine Thysanoptera associated with domicile-building thrips on *Acacia* trees. *Australian Journal of Entomology*, vol. 39, no. 3, pp. 130-137. http://dx.doi.org/10.1046/j.1440-6055.2000.00165.x.

RAMAMURTHY, V.V., 2007. Faunistic, ecological, biogeographical and phylogenetic aspects of Coleoptera as gall-inducers and associates in plant galls in the Orient and eastern Palearctic. *Oriental Insects*, vol. 41, no. 1, pp. 93-119. http://dx.doi.org/10.1080/00305316.2007.10417501.

REDFERN, M. and ASKEW, R.R., 1992. *Plant galls*. Slough: Richmond Publishing. Naturalists' Handbooks, no. 17.

RIBEIRO, A.N., BALBI, M.I.P.A. and URSO-GUIMARÃES, M.V., 2019. Characterization of insect galls from a vegetation area in Altinópolis, São Paulo State, Brazil. *Papéis Avulsos de Zoologia*, vol. 59, e20195904. http://dx.doi.org/10.11606/1807-0205/2019.59.04.

RODRIGUES, A.R., MAIA, V.C. and COURI, M.S., 2014. Insect galls of restinga areas of Ilha da Marambaia, Rio de Janeiro, Brazil. *Revista Brasileira de Entomologia*, vol. 58, no. 2, pp. 173-197. http://dx.doi.org/10.1590/S0085-56262014000200010.

SAITO, V.S. and URSO-GUIMARÃES, M.V., 2012. Characterization of galls, insect galls and associated fauna of Ecological Station of Jataí (Luiz Antônio, SP). *Biota Neotropica*, vol. 12, no. 3, pp. 1-9. http://dx.doi.org/10.1590/S1676-06032012000300011.

SANTOS, B.B., FERREIRA, H.D. and ARAÚJO, W.S., 2010. Ocorrência e caracterização de galhas entomógenas em uma área de floresta estacional semidecídua em Goiânia, Goiás, Brasil. *Acta Botanica Brasílica*, vol. 24, no. 1, pp. 243-249. http://dx.doi.org/10.1590/S0102-33062010000100026.

SANTOS, I.S., LIMA, V.P., SOARES, E.K.S., PAULA, M. and CALADO, D.C., 2018. Insect galls in three species of *Copaifera* L. (Leguminosae, Caesalpinioideae) occurring sympatrically in a Cerrado area (Bahia, Brazil). *Biota Neotropica*, vol. 18, no. 1, pp. e20170356. http://dx.doi.org/10.1590/1676-0611-bn-2017-0356.

SANTOS, J.C., RIBEIRO, B.A., SILVA, T.M. and ARAUJO, W.S., 2012. Galhas de insetos em uma área de cerrado sentido restrito na região semi-urbana de Caldas Novas (Goiás, Brasil). *Revista Brasileira de Biociências*, vol. 10, no. 4, pp. 439-445.

SILVA, A.R.F., NOGUEIRA, R.M., COSTA, E.C., CARVALHO-FERNANDES, S.P. and SANTOS-SILVA, J., 2018a. Occurrence and characterization of entomogenic galls in an area of Cerrado *sensu stricto* and Gallery forest of the state of Bahia, Brazil. *Anais da Academia Brasileira de Ciências*, vol. 90, no. 3, pp. 2903-2919. http://dx.doi.org/10.1590/0001-3765201820170522. PMid:30304224.

SILVA, E.C., SANTOS, B.B. and ARAÚJO, W.S., 2018b. Insect gall occurrence in savanna and forest remnant sites of Hidrolândia, GO, Brazil Central. *Papéis Avulsos de Zoologia*, vol. 58, e20185804. http://dx.doi.org/10.11606/1807-0205/2018.58.04.

UESUGI, A., MORRELL, K., POELMAN, E.H., RAAIJMAKERS, C.E. and KESSLER, E., 2016. Modification of plant-induced responses by an insect ecosystem engineer influences the colonization behaviour of subsequent shelter-users. *Journal of Ecology*, vol. 104, no. 4, pp. 1096-1105. http://dx.doi.org/10.1111/1365-2745.12587.

URSO-GUIMARÃES, M.V., SCARELI-SANTOS, C. and BONIFÁCIO-SILVA, A.C., 2003. Occurrence and characterization of entomogen galls in plants from natural vegetation areas in Delfinópolis, MG, Brazil. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, vol. 63, no. 4, pp. 705-715. http://dx.doi.org/10.1590/S1519-69842003000400018. PMid:15029382.

VIEIRA, L.G., NOGUEIRA, R.M., COSTA, E.C., CARVALHO-FERNANDES, S.P. and SILVA, J.S., 2018. Insect galls in Rupestrian field and Cerrado *stricto sensu* vegetation in Caetité, Bahia, Brazil.

Biota Neotropica, vol. 18, no. 2, pp. e20170402. http://dx.doi.org/10.1590/1676-0611-bn-2017-0402.

WETZEL, W.C., SCREEN, R.M., LI, I., MCKENZIE, J., PHILLIPS, K.A., CRUZ, M., ZHANG, W., GREENE, A., LEE, E., SINGH, N., TRAN, C. and YANG, L.H., 2016. Ecosystem engineering by a gall-forming wasp indirectly suppresses diversity and density of herbivores on oak trees. *Ecology*, vol. 97, no. 2, pp. 427-438. http://dx.doi.org/10.1890/15-1347.1. PMid:27145617.