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

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

V. C. Maia*  
*Unividade Federal do Rio de Janeiro – UFRJ, Museu Nacional, Departamento de Entomologia, Rio de Janeiro, RJ, Brasil

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. Cecidophages 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 induzidor, modificação dos tecidos da galha ou produção de novos tecidos, relação filogenética com o induzidor 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 géneros de 24 famílias vegetais, totalizando 65 registros. A maioria dos inquilinos foi reposicionada na guilda dos cecidófagos e outros na guilda dos kleptoparasitas, 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 kleptoparasitas foram representados apenas por 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, kleptoparasitas, 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;
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, Sciariidae, and Tephritidae), Coleoptera, Hemiptera (Aphididae, Coccidae, and Tingidae), Hymenoptera (Eulophidae, Formicicidae 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 morphosppecies 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.

| Family           | Host Plant                  | Gall-inducer                      | Inquiline                                | Reference |
|------------------|-----------------------------|-----------------------------------|------------------------------------------|-----------|
| Anacardiaceae    | Atronium sp.                | Hemiptera                         | Clinodiplosis sp. (Cecidomyiidae)       | Maia (2013) |
|                  | Asteraceae                  | Mikania cf. biformis DC.          | Contarinia ubiquita Gagné, 2001 (Cecidomyiidae) | Maia et al. (2008) |
|                  |                             | Liodiplosis conica Gagné, 2001   | Trotteria sp. (Cecidomyiidae)           | Maia et al. (2008) |
|                  |                             | Liodiplosis conica Gagné, 2001   | 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) |
| Liodiplosis conica Gagné, 2001 |                   | Asphondyla sp.                    | Lepidoptera and Curculionidae (Coleoptera) | Maia et al. (2008) |
| Porophyllum ruderale (Jack.) Cass. |                       | Neolasioptera sp.                 | Trypaneus sp. (Diptera, Tephritidae)     | Rodrigues et al. (2014) |
| Bignoniaceae     | Parabignonia unguiculata (Vell.) A. H. Gentry |                      | Resseliella sp. (Cecidomyiidae)         | Maia et al. (2008) |
| Boraginaceae     | Varronia curassavica Jacq. | Lopesini (Cecidomyiidae)          | Curculionidae (Coleoptera)               | Maia et al. (2008) |
| Calophyllaceae   | Calophyllum brasiliense Cambess. |                          | Lopesia elliptica Maia, 2003 (Cecidomyiidae) | Maia et al. (2008) |
| Celastraceae     | Elachyptera micrantha (Cambess.) A. C. Sm. |                     | Lopesia indaiensis (Cecidomyiidae)      | Maia et al. (2008) |
| Erythroxylaceae  | Erythroxylum ovalifolium Peyrs |                          | Lopesia erythroxyli Rodrigues and Maia, 2010 | 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) |
| Andira nitida Mart. ex Benth. |            | Asphondyliina                    | Curculionidae (Coleoptera)               | Maia et al. (2008) |
| Inga laurina (Sw.) Willd. |                   | Neolasioptera sp. (Cecidomyiidae) | Lepidoptera                              | Rodrigues et al. (2014) |
| Inga sp.         |                             | Neolasioptera sp. (Cecidomyiidae) | Lepidoptera                              | Rodrigues et al. (2014) |
| Lauraceae        | Ocotea lobii (Meisn.) Rohwer | Ceclidiomyiidae                  | Curculionidae (Coleoptera)               | Maia et al. (2008) |
| Ocotea notata (Nees & Mart.) Mez |                  | Not determined                    | Trotteria sp. (Cecidomyiidae)           | Maia et al. (2008) |
| Lamiaceae        | Hyptis fasciculata Benth.   | Ceclidiomyiidae                  | Curculionidae (Coleoptera)               | Maia et al. (2008) |
| Maia & Oliveira, 2018 |              | Asphondyliina                    | Curculionidae (Coleoptera)               | Maia et al. (2008) |
| Inga sp.         |                             | Neolasioptera sp. (Cecidomyiidae) | Lepidoptera                              | Rodrigues et al. (2014) |
| Lauraceae        | Ocotea lobii (Meisn.) Rohwer | Ceclidiomyiidae                  | Curculionidae (Coleoptera)               | Maia et al. (2008) |
| Ocotea notata (Nees & Mart.) Mez |                  | Not determined                    | Trotteria sp. (Cecidomyiidae)           | Maia et al. (2008) |
| Lauraceae        | Ocotea lobii (Meisn.) Rohwer | Ceclidiomyiidae                  | Curculionidae (Coleoptera)               | Maia et al. (2008) |
| Bregonci et al. (2010) |                  | Asphondyliina                    | Curculionidae (Coleoptera)               | Maia et al. (2008) |
Table 1. Continued...

| Family         | Host Plant                      | Species            | Gall-inducer       | Inquiline                  | Reference                   |
|----------------|---------------------------------|--------------------|--------------------|---------------------------|-----------------------------|
| Loranthaceae   | Ocotea pulchella (Nees) Mez     |                    | Cecidomyiidae      | Hemiptera                 | Maia et al. (2008)          |
|                |                                  |                    | Not determined     | Trotteria sp.             | Maia et al. (2008)          |
|                | Struthanthus concinnus Mart.    |                    | Asphondylia sp.    | Cecidomyiidae and         | Rodrigues et al. (2014)     |
|                |                                  |                    | (Cecidomyiidae)    | Thysanoptera              |                             |
| Malvaceae      | Luehea divaricata Mart          |                    | Cecidomyiidae      | Ocella sp. (Chloropidae,  | Rodrigues et al. (2014)     |
| Melastomataceae| Miconia cinnamomifolia (DC.)   |                    | Euphormyonia       | Reselliella sp. (Cecidomyiidae) | Maia (2001)               |
|                | Naudin.                         |                    | miconta Maia, 2001 |                           |                             |
|                | Tibouchina trichopoda (DC.)    |                    | Cucurbitaceae      | Curculionidae (Coleoptera)| Maia et al. (2008)          |
|                | Ball.                           |                    |                    |                           |                             |
| Myrtaceae      | Campomanesia guaviroba (DC.)   |                    | Clinodiplosis sp.  | Membracidae (Hemiptera)  |                             |
|                | Klaersk.                        |                    | (Cecidomyiidae)    |                           |                             |
|                | Eugenia astringens Cambess.     |                    | Euphormyonia        | Leia (Cecidomyiidae)     |                             |
|                |                                 |                    | rotundiflorum      | Maia, 1994                | Maia (1995)                 |
|                |                                  |                    |                    |                           |                             |
|                | Eugenia copacabanensis Klaersk. |                    | Euphormyonia        | Leia (Cecidomyiidae)     |                             |
|                |                                 |                    | rotundiflorum      | Maia, 1994                | Maia (1995)                 |
|                | Eugenia hiemalis Cambess.       |                    | Euphormyonia        | Leia (Cecidomyiidae)     |                             |
|                |                                 |                    | sp.                 | Maia, 1994                | Maia (1995)                 |
|                | Eugenia punicifolia (Kunt) DC.  |                    | Not determined      | Curculionidae (Coleoptera)| Rodrigues et al. (2014)     |
|                |                                  |                    |                    |                           |                             |
|                | Eugenia speciosa Cambess.       |                    | Schizomyiina        | Sannosa (Butler, 1877)    | Personnal observation       |
|                |                                  |                    | Clinodiplosis sp.  |                           |                             |
|                |                                  |                    | (Cecidomyiidae)     |                           |                             |
|                | Myrcia ovata Cambess.           |                    | Myrciamyia         |                           |                             |
|                |                                  |                    | maricaensis Maia, 1995 |                           |                             |
|                | Myrciaria floribunda (H.West ex |                    | Euphormyonia        |                           |                             |
|                | Wild.l.) O. Berg.               |                    | sp.                 |                           |                             |
|                | Neomitranthes obscura (DC.) N. |                    | Euphormyonia        |                           |                             |
|                | J. E. Silveira                   |                    | rotundiflorum      |                           |                             |
|                |                                  |                    | Maia, 1996          |                           |                             |
|                |                                  |                    | Euphormyonia        |                           |                             |
|                |                                  |                    | sp.                  |                           |                             |
| Nyctaginaceae  | Guapira opposita (Vell.) Reitz  |                    | Brugmannia elongata | Lepidoptera               | Maia et al. (2008)          |
|                |                                  |                    | Maia & Couri, 1993 |                           |                             |
|                |                                  |                    | (Cecidomyiidae)     |                           |                             |
|                |                                  |                    | Brugmannia sp.      | Lepidoptera               | Rodrigues et al. (2014)     |
|                |                                  |                    | (Cecidomyiidae)     |                           |                             |
|                |                                  |                    | Pisphondylia sp.    | Lepidoptera               | Rodrigues et al. (2014)     |
|                |                                  |                    |                    |                           |                             |
| Ochnaceae      | Guapira pernambucensis (Casar.) |                    | Cecidomyiidae      | Lepidoptera               | Bregonci et al. (2010)       |
|                | Lundell                         |                    |                    |                           |                             |
|                | Ouratea cuspidata (A.St.-Hil.)  |                    | Cecidomyiidae      | Lepidoptera               | Bregonci et al. (2010)       |
|                | Engl.                           |                    |                    |                           |                             |
| Peraceae       | Chaetocarpus myrsinites Baill.   |                    | Cecidomyiidae      | Lepidoptera               | Bregonci et al. (2010)       |
| Polygalaceae   | Securidaca sp.                  |                    | Cecidomyiidae      | Muscomorpha (Diptera)     | Rodrigues et al. (2014)     |
Fauna associated with galls

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%).

Table 1. Continued...

| Family            | Host Plant | Gall-inducer | Inquiline | Reference                  |
|-------------------|------------|--------------|-----------|----------------------------|
| Polygonaceae      | Coccoloba alnifolia Casar | Lopesia sp. | Lepidoptera | Rodrigues et al. (2014)    |
| Sapindaceae       | Paullinia weinmannifolia Mart. | Paulliniomyia ampla Maia, 2001 (Cecidomyiidae) | Eulophidae (endogaller) | Maia (2001)                |
|                   | Paullinia sp. | Neolasioptera sp. (Cecidomyiidae) | Lepidoptera | Maia et al. (2008)         |
|                   | Serjania communis Cambess. | Cinodiplosis 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)                |
|                   | Pouteria caimito (Ruíz & Pav.) Radlk. | Youngomyia pouteriae Maia, 2001 (Cecidomyiidae) | Coleoptera | Bregoni et al. (2010)     |
|                   | Sideroxylon obtusifolium (Roem. & Schult.) T. D. Penn. | Bruggmannniella sideroxyli Rodrigues & Maia, 2020 | Cecidomyiidae | Rodrigues et al. (2014)    |
| Solanaceae        | Aureliana fasciculata (Vell.) Sendtn. | Cinodiplosis sp. (Cecidomyiidae) | Curculionidae (Coleoptera) | Maia et al. (2008)         |
|                   | 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, Cinodiplosis 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 cecidomyiidi 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 species | Number of gall morphotypes | Number of records of inquilines |
|------------|-------------------|----------------------------|---------------------------------|
| 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 aphids, 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 globose 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, Tephritidae), Hymenoptera (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. | *Clinodiplosis annulipes* Gagné, 2001 | *Contarinia ubiquita* Gagné, 2001 |
| *Baccharis singularis* (Vell.) G. M. Barroso | *Liodiplosis conica* Gagné, 2001 | *Trotteria* sp. (kleptoparasite) |
| *Baccharis speciosa* DC. | Neolasioptera sp. | Thysanoptera (cecidophage) |
| *Piptocarpa* cf. *cinerea* Baker | Cecidomyiidae | Lepidoptera (cecidophage) |
| *Porophyllum ruderale* (Jack.) Cass. | Asphondyliina | Lepidoptera (cecidophage) |
| *Parabignonia unguiculata* (Vell.) A. H. Gentry | *Cecidomyiidae* | Resseliella sp. (kleptoparasite) |
| *Varronia curassavica* Jacq. | Lopesiini | Curculionidae (cecidophage) |
| *Calophyllum brasilense* Cambess. | *Lopesia elliptica* Maia, 2003 | Coleoptera (cecidophage) |
| *Elachyptera micrantha* (Cambess.) A. C. Sm. | *Cecidomyiidae* | Lepidoptera (cecidophage) |
| *Erythroxylum ovalifolium* Peyrs. | *Lopesia erythroxyl* Rodrigues and Maia, 2010 | Eulophidae (inquiline) |
| *Croton compressus* Lam. | Not determined | Curculionidae (cecidophage) |
| *Andira* fraxinifolia Benth. | *Cecidomyiidae* | Curculionidae and Lepidoptera (cecidophages) |
| *Ocotea lobbii* (Meisn.) Rohwer | Hemiptera | Cucurbitidae (cecidophage) |
| *Ocotea notata* (Nees & Mart.) Mez | *Cecidomyiidae* | Lepidoptera (cecidophage) |
| *Ocotea pulchella* (Nees) Mez | Not determined | *Trotteria* sp. (kleptoparasite) |
| *Struthanthus concinnus* Mart. | *Cecidomyiidae* | *Cecidomyiidae* (kleptoparasite) and Thysanoptera (cecidophage) |
| *Luehea divaricata* Mart. | Asphondyliina | Lepidoptera (cecidophage) |
| *Miconia cinnamomifolia* (DC.) Naudin. | Epihormomyia miconiae Maia, 2001 | Eulophidae (inquiline) |
| *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 tetraloba* Maia, 1994 | *Trotteria* sp. (kleptoparasite) |
| *Eugenia hiemalis* Cambess. | Stephomyia sp. | Leptothorax sp. (successor) |
| *Eugenia punicifolia* (Kunt) DC. | Not determined | Curculionidae (cecidophage) |
| *Myrcia ovata* Cambess. | Schizomyiina | Sciariidae (cecidophage) |
| *Myrtiaria floribunda* (H. West ex Willd.) O. Berg | *Cecidomyiidae* | *Eulophidae* sp.1 and *Eulophidae* sp. 2 (inquilines) |
| *Neomitrantes obscursa* (DC.) N. J. E. Silveira | Neomitrantes robusta Maia, 2001 | *Trenora annosa* (Butler, 1877) (cecidophage) |
Table 4. Continued...

| Host Plant                                      | Gall-inducers                  | Associated fauna               |
|------------------------------------------------|--------------------------------|--------------------------------|
| Guapira opposita (Vell.) Reitz                 | Clinodiplosini                | Stenoma annosa (cecidophage)   |
| Bruggmannia elongata Maia & Couri, 1993        |                                |                                |
| Bruggmannia sp.                                |                                |                                |
| Pisphodylia sp.                                |                                |                                |
| G. pernambucensis (Catar.) Lundell             | Cecidomyiidae                 | Lepidoptera (cecidophage)      |
| Ouratea cuspidata (A.St.-Hil.) Engl.           | Contarinia sp.                | Coleoptera (cecidophage)       |
| Chaetocarpus myrsinates Baill.                 | Not determined                | Lepidoptera (cecidophage)      |
| Securidaca sp.                                 | Cecidomyiidae                 | Muscomorpha (cecidophage)      |
| Coccoloba a Frips. Casar                       | Lopesia sp.                   | Lepidoptera (cecidophage)      |
| Paulinia weinmannifolia Mart.                  | Pualliniacyampa ampla, 2001    | Eulophidae (inquiline)         |
| Paulinia sp.                                   |                                |                                |
| Serjania communis Cambess.                     | Clinodiplosis sp.             | Sciaridae (cecidophage)        |
| Pouteria venosa (Mart.) Baehni                 | Lopesia singularis, 2001       | Lepidoptera (cecidophage)      |
| Manilkara subsericea (Mart.) Dubard            | Cecidomyiidae                 | Contarinia sp. (kleptoparasite) |
| Pouteria cainito (Ruiz & Pav.) Radlk.          | Youngomyia pouteriae, 2001     | Coleoptera (cecidophage)       |
| Sideroxylon obtusifolium (Roem. & Schult.) T. D. | Bruggmanniella sideroxyl     | Cecidomyiidae (kleptoparasite) |
| Aureliana fasciculata (Vell.) Sendtn.          | Clinodiplosis sp.             | Curculionidae (cecidophage)    |
| Stachytarpheta sp.                             | Schizomyia stachytarphetae, 1932| Haplothrips gowdeyi, (Franklin, 1908) |

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

| Guilds          | Inquilines                | Host plant                  | Host organ | Shape  | Color  | Trichomes |
|-----------------|---------------------------|----------------------------|------------|--------|--------|-----------|
| Eulophidae      | Erythroxylum ovalifolium Peyrs. | Bud                        | Conical    | Green  | Absent |
| Eulophidae sp.1 | Myrica ovata Cambess.     | Bud                        | Cylindrical| Brown  | Absent |
| Eulophidae sp. 2| Myrica ovata              | Bud                        | Ovoid      | Green  | Absent |
| Eulophidae      | Paulinia weinmannifolia Mart. | Leaf                      | Conical    | Green  | Absent |
| Kleptoparasites | Andira fraxinifolia Benth. | Leaf                      | Vermiform  | Green  | Absent |
| Cedicomyiidae   | Struthanthus concinnus Mart. | Leaf and stem              | Conical    | Green  | Absent |
| Cedicomyiidae   | Sideroxylon obtusifolium (Roem. & Schult.) T. D. Penn. | Fruit  | Globoid  | Green  | Absent |
| Contarinia ubi    | 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 cinnamonifolia (DC.) Naudin. | Bud | Ovoid    | Green  | Absent |
Table 5. Continued...

| Guilds                        | Host plant                  | Inquilines                | Host organ | Shape    | Color   | Trichomes |
|-------------------------------|-----------------------------|---------------------------|------------|----------|---------|-----------|
| Tanaostigmatidae              | *Inga laurina* (Sw.) Willd. | Trotteria quadridentata   | Leaf       | Cylindrical | Yellow | Absent    |
| *Pouteria caimito* (Ruiz & Pav.) Radlk. |                  | Trotteria sp.             | Leaf       | Conical   | Green   | Absent    |
| *Ocotea lobbia* (Meisn.) Rohwer |                | Trotteria sp.             | Leaf and stem | Conical   | Green   | Absent    |
| *Ocotea pulchella* (Nees) Mez |                | Trotteria sp.             | Stem       | Fusiform   | Brown   | Absent    |
| *Eugenia copacabanensis* Klaersk. |           | Trotteria sp.             | Leaf       | Fusiform   | Red     | Absent    |
| Coccidophages                 |                            |                            |            |           |         |           |
| Clinodiplosis sp.             | *Atronium* sp.              | Thysanoptera              | Leaf       | Globoid   | Green   | Absent    |
| *Baccharis singularis* (Vell.) G. M. Barroso |            |                            | Leaf and stem | No data | No data | No data |
| Acanthocheilla sp. (Tingidae, Hemiptera) | |                            |            |           |         |           |
| *Mikania cf. biformis* DC.    |                            | Acanthocheilla sp. (Hemiptera) | Leaf       | Globoid   | Green   | Absent    |
| Aphididae (Hemiptera)         |                            |                            | Leaf       | Globoid   | Green   | Absent    |
| Coccidae (Hemiptera)          | *Mikania cf. biformis* DC.  |                            | Leaf       | Globoid   | Green   | Absent    |
| Curculionidae (Coleoptera)    | *Mikania cf. biformis* DC.  |                            | 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* Baker |                            | Leaf petiole, stem, bud | Globoid | Brown   | Absent    |
| Lepidoptera                   | *Piptocarpha cf. cinerea* Baker |                        | Leaf petiole, stem, bud | Globoid | Brown   | Absent    |
| *Trypanea* sp.                | *Porophyllum ruderale* (Jack.) Cass. | Curculionidae | Inflorescence | Fusiform | Green   | Absent    |
| Curculionidae                 | *Varronia curassavica* Jacq. |                            | Leaf vein | Fusiform   | Green   | Absent    |
| Coleoptera                    | *Calophyllum brasiliense* Cambess. | Curculionidae | Leaf       | Fusiform   | Green   | Absent    |
| Lepidoptera                   | *Elachyptera micranta* (Cambess.) A. C. Sm. | Curculionidae | Leaf and bud | Conical   | Green   | Absent    |
| Curculionidae                 | *Croton compressus* Lam.    | Curculionidae              | Inflorescence | Amorphous | Yellow | Present   |
| Curculionidae                 | *Andira fraxinfolia* Benth. | Curculionidae              | Leaf       | Vermiform | Green   | Absent    |
| Lepidoptera                   | *Andira fraxinfolia*        | Curculionidae              | Leaf       | Vermiform | Green   | Absent    |
| Curculionidae                 | *Andira fraxinfolia*        | Curculionidae              | Leaf       | Vermiform | Green   | Absent    |
| Coleoptera                    | *Andira nitida* Mart. ex Benth | Curculionidae | Leaf       | Lenticular | Green   | Absent    |
| Lepidoptera                   | *Inga* sp.                  |                            | Stem       | Fusiform   | Green, Brown | Present |
| Curculionidae                 | *Hyptis fasciculata* Benth. | Curculionidae              | Leaf vein, petiole and stem | Fusiform | Green, brown | Absent |
| Cecidomyiidae                 | *Ocotea notata* (Nees & Mart.) Mez | Membracidae | Leaf       | Lenticular | Green, yellow | Absent |
| Hemiptera                     | *Ocotea pulchella* (Nees) Mez |                            | Leaf and bud | Fusiform | No data | Absent    |
| Thysanoptera                  | *Struthanthus concinnus* Mart. |                            | Leaf and stem | Conical   | Green   | Absent    |
| Olea sp.                      | *Luehea divaricata* Mart.   |                            | Stem       | Globoid   | Brown   | Absent    |
| Curculionidae                 | *Tibouchina trichopoda* (DC.) Baill. | Curculionidae | Stem       | Fusiform   | Brown   | Absent    |
| Membracidae                   | *Campomanesia guaviroba* (DC.) Klaersk. | Membracidae | Leaf vein | Globoid   | No data | Absent    |
Table 5. Continued...

| Guilds         | Host plant                   | Inquilines                   | Host organ | Shape     | Color         | Trichomes |
|----------------|------------------------------|------------------------------|------------|-----------|---------------|-----------|
| Curculionidae  | *Eugenia paniculata* (Kunt) DC. | **Stenoma annosa** (Lepidoptera) | Fruit      | Globoid   | Green, yellow, Red | Absent    |
| Sciariidae     | *Eugenia speciosa* Cambess. | **Stephomyia rotundifoliorum** (Diptera) | Leaf       | Conical   | Yellow         | Absent    |
| Thysanoptera   | *Myrcia floribunda* (H.West ex Willd.) | **Lepidoptera** Guapira opposita (Vell.) Reitz | Leaf       | Globoid   | Green          | Present   |
| Stenoma annosa | *Neomitrantes obscura* (DC.) N. J. E. Silveira | **Lepidoptera** Guapira opposita | Leaf       | Marginal roll | Green   | Absent    |
| Sciaridae      | *Neomitrantes obscura* | **Lepidoptera** Guapira opposita | Bud        | Conical | Green          | Absent    |
| Thysanoptera   | *Myrcia floribunda* (H.West ex Willd.) | **Aphididae** Guapira opposita | Leaf       | Lenticular | Green          | Absent    |
| Stenoma annosa | *Neomitrantes obscura* | **Lepidoptera** Guapira opposita | Leaf       | Globoid | Brown          | Absent    |
| S. annosa      | *Neomitrantes obscura* | **Lepidoptera** Guapira opposita | Flower peduncle | Globoid | Green, Brown, red | Absent    |
| Lepidoptera    | *Guapira pernambucensis* (Casar.) Lundell | **Lepidoptera** Guapira opposita | Leaf       | Lenticular | Green, Brown | Absent    |
| Coleoptera     | *Ouratea cuspidata* (A.St.-Hil.) Engl. | **Lepidoptera** Chaetocarpus myrsinites Baill. | Leaf       | Conical | Brown          | Absent    |
| Lepidoptera    | *Chaetocarpus myrsinites* Baill. | **Lepidoptera** Chaetocarpus myrsinites Baill. | Leaf       | Lenticular | Green, Brown | Absent    |
| Muscomorpha    | *Securidaca* sp. | **Lepidoptera** Cocclobo ahiifolia Casar | Closed flower | Ovoid | Purple | Absent    |
| Lepidoptera    | *Cocclobo ahiifolia* Casar | **Lepidoptera** Chaetocarpus myrsinites Baill. | Inflorescence | Globoid | Green, Yellow | Absent    |
| Lepidoptera    | *Paulinia* sp. | **Lepidoptera** Chaetocarpus myrsinites Baill. | Leaf petiole, vein and tendril | Fusiform | Green | Absent    |
| Sciariidae     | *Serjania communis* Cambess. | **Lepidoptera** Chaetocarpus myrsinites Baill. | Bud        | Ovoid    | Red            | Absent    |
| Lepidoptera    | *Pouteria venosa* (Mart.) Baehni | **Lepidoptera** Chaetocarpus myrsinites Baill. | Leaf       | Globoid  | Green          | Absent    |
| Coleoptera     | *Manilkara subservica* (Mart.) Dubard | **Lepidoptera** Chaetocarpus myrsinites Baill. | Leaf       | Lenticular | Green          | Absent    |
| Curculionidae  | *Aureliana fasciculata* (Vell.) Sendtn. | **Lepidoptera** Chaetocarpus myrsinites Baill. | Leaf vein | Fusiform | Green          | Absent    |
| Haplothrips    | **Haplothrips gowdeyi** | **Lepidoptera** Chaetocarpus myrsinites Baill. | 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), *Acanthochella* (Tingidae), *Trypanea* (Tephritidae), and *Occella* (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 erythroxylif* 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 weinmannifolia* Mart. (Sapindaceae) and the other induced by *M. maricaensis* on *Myrcia ovata* (Figures 3 and 4). None of these inquilines...
Trotteria (Cecidomyiidae), Tavares, 1916, sp.: Tephritidae) and , and , sp.). Galls induced by Kieffer, 1894, hosted only Tavares, 1906. Membracids, sciarids and Rübsaamen, 1908, hosted . Representatives of Diptera Felt, 1908, Loew, 1850, and .

3.2.4. Kleptoparasites (Myrtaceae). These two cases are probably the same. Successor in similar galls on not be considered cecidophagous since it did not feed on gall tissues. 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 vermiciform 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 Rūbšačen, 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 Clinidiplosis Kieffer, 1894, hosted only cecidophages, as did those induced by species of Neolasioptera Felt, 1908, Asphondylia Loew, 1850, and Brugmannia 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 Trypaneae sp.: Tephritidae) and Thysanoptera were obtained from galls of Asphondylia,
whereas representatives of Hemiptera (Aphididae) and Lepidoptera were obtained from galls of Brugmannia. 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. biforments*, *Andira fraxinifolia* (Fabaceae), *Guapira opposita* (Nyctaginaceae), *Piptocarpha cf. cinerea*, and *Neomitrantes obscura* (Myrtaceae) were the plant taxa with the richest cecidophagus 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 cecidophagus 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).

Cecidophages 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 (Lourengo 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, cecidophagus 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 (Usukie et al., 2016).

The taxonomic knowledge of cecidophagus, 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.

Acknowledgements

This research was supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (Proc. 301481/2017-2).

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