Guilds in Insect Galls: Who is Who

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Guilds in insect galls: who is who

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Abstract

Evolutionary and biological patterns can be obscured by inadequate or ill-defined terminology, especially when referring to ecological interactions. For example, cecidogenous (gall-inducing) species are considered ecosystem engineers, promoting structures rich in nutrients that create distinct microhabitats with many organisms interacting with the galls and gall inducers. These interactors are classified as members of a guild, and are described according to location, attribute, or activity of the host species. Guilds often do not typically have strict or clearly defined boundaries, nor do they need to be taxonomically interconnected. Cecidophage, inquilines, and kleptoparasite guilds appear to be poorly understood and misinterpreted. Herein, we bring an overview of the features that might help conceptualize and differentiate these interactions. We suggest that some cases described in the literature might be reassessed, and clear criteria proposed to distinguish among these 3 guilds associated with galls.

Key Words: terminology; associated guild; successor; inquilinism; cecidophagy

Resumo

Padrões biológicos e evolutivos podem ser obscurecidos pelo uso inadequado ou mal definido de conceitos biológicos, por exemplo, na definição de interações ecológicas. Neste contexto, encontramos na literatura de galhas um evidente problema de terminologia. Galhadores são considerados engenheiros de ecossistemas, promovendo uma estrutura rica em nutrientes e com um micro-habitat próprio que inexiste normalmente na planta. Por esta causa, encontramos diversos organismos interagindo com as galhas e com os galhadores. Estas interações são divididas em guildas associadas às galhas, e nessa divisão em guildas é onde está o problema. As guildas de cecidófagos, inquilinos e cleptoparasitas são ainda mal compreendidas e interpretadas. Sendo assim, neste estudo trazemos características que auxiliam na conceituação e distinção dessas interações entre si. Sugerimos que alguns casos descritos na literatura sejam revistos e que sejam usados os critérios aqui propostos para diferenciar estas 3 guildas associadas às galhas.

Palavras Chaves: terminologia; guildas associadas; sucessor; inquilinismo; cecidofagia

Galls are alterations in plant tissue due to feeding or other stimuli induced by organisms such as insects, mites, and viruses, among others (Dreger-Jauffret & Shorthouse 1992); however, insects are the most common cause (Maia & Fernandes 2004). Hypertrophy and hyperplasia in plant cells bring about changes (Dreger-Jaufret & Shorthouse 1992), resulting in the formation of gall tissues that are rich in nutrients and consequently possess a higher nutritional value than the original host plant tissue (Price et al. 1987).

Because of nutrient richness and ability to provide a differentiated microhabitat, galls serve as a resource for many organisms. In addition, galls house the inducer while serving as a resource for its natural enemies. However, the gall system encompasses a complex web of organisms that interact with each another and have been referred to as guilds (Mani 1964; Sanver & Hawkins 2000).

Sugiura and Yamazaki (2009) constructed a brief conceptual review of these guilds with an emphasis on Coleopteran and Lepidopteran cecidophages. These guilds can be divided into 2 groups: organisms that interact with galls and can interact secondarily with the inducer, and those that interact directly with the inducer. The first group can be separated into inquilines, cecidophages, and successors. The second would be predators, parasitoids, symbionts, and kleptoparasites (Fig. 1, adapted from Sugiura & Yamazaki 2009). Among all these organisms, predators, parasitoids, symbionts, and successors appear to be well delimited in the literature. Nevertheless, 3 groups of organisms interacting inside a gall structure may appear to have confusing roles due to terminological problems.

Predators and parasitoids are some of the culprits responsible for gall-inducer mortality. Birds and various insects can be gall-inducer predators (Craig et al. 2007), whereas several parasitoids (e.g., Chalcidoidea, Ichneumonoidea) are known for attacking the immatures of gall inducers (Stone et al. 2002). Ecologically, parasitoids are reported as the primary top-down control for populations of gall-inducing in-

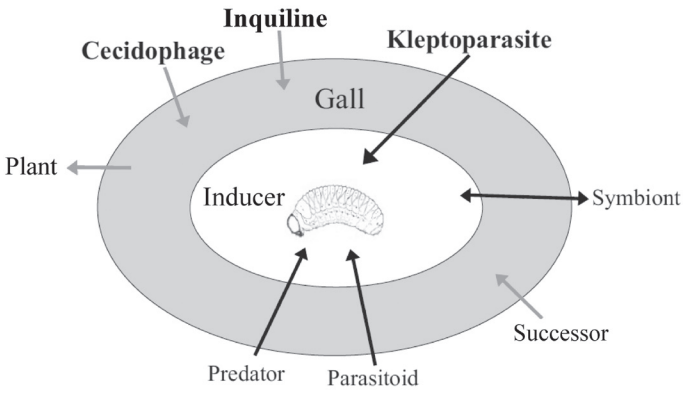

Fig. 1. Organism guilds associated with galls and gall inducers. Gray arrows represent interaction with the gall, black arrows with the inducer (modified from Sugiura & Yamazaki 2009).

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sects (Toma & Mendonça 2014). Their role appears to be clear and unequivocal, interacting in a straightforward manner with gallers only (trophically), although parasitoids can end up using the gall as a refuge in the process as well.

Successors are organisms that use the gall after the inducer leaves it (Mani 1964). These are very common in conspicuous galls that remain connected to plants over a long period of time; these organisms are mostly mites, spiders, thrips, beetles, and springtails. They apparently use gall tissues for food and shelter, but dead or decaying gall tissue is probably attacked by fungi that also serve as food. Successors may form specific food webs within the abandoned gall and are clear examples of the engineering effect that gallers have on host plants (Sanver & Hawkins 2000).

Inquilines and cecidophages are incapable of producing their own galls but feed off gall tissues (Mani 1964). Inquilines install themselves on galls in a way that might or might not be fatal to the inducers and may prompt the formation of new gall tissue. Cecidophages, on the other hand, simply consume gall tissues. Like inquilines, they do not attempt to kill the inducer; however, they are unable to promote the production of new tissues (Caltagirone 1964). Kleptoparasitism is the theft of a resource (i.e., the gall) by another organism that can be initiated by the abandonment of a gall or death of the gall inducer (Mound & Morris 2000). Figure 1 illustrates this interaction between guilds associated with the gall/gall-inducing system. Previous characterizations of these 3 gall-associated guilds have appeared to be too broad even though different literature sources have frequently used them distinctly, often without adequate criteria. Herein, we endeavor to provide a more complete conceptual definition of these guilds that incorporates clear and unambiguous terminology in order to allow for its consistent use in the literature.

DIFFERENTIATING CECIDOPHAGES, INQUILINES, AND KLEPTOPARASITES

Previously, the context of galls and their interactions with inquilines and cecidophages were characterized by Mani (1964) within an evolutionary context. This author pointed out that inquilines must have acquired their habits from gall-inducing ancestors, whereas cecidophages evolved independently. On the other hand, Mound and Morris (2000) studied kleptoparasitic thrips of other gall-inducing thrips and reported that the kleptoparasites killed the gall inducers; this was not the case for inquiline thrips that do not disturb the inducer.

Although the works cited above provide some tools for distinguishing among the guilds, none use multiple non-superposed parameters capable of completely differentiating organisms into one or the other category. In contrast, we propose the use of 5 interaction parameters: food habit; coexistence with the inducer; production of new tissues; phylogenetic relationship with the inducer; and mobility obtained from the literature to conceptualize and differentiate cecidophages, inquilines, and kleptoparasites from each other. A summary of the information is presented in Table 1.

FOOD HABIT

Food habit is the primary characteristic that separates kleptoparasitism from the other 2 interactions. Cecidophages and inquilines are exclusively phytophages (Caltagirone 1964; Ronquist 1994), whereas kleptoparasites interact directly with the inducer, and when they do not chase the inducer away, they kill it, demonstrating omnivorous habits (Mound & Morris 2000; Luz et al. 2015).

Table 1. Parameters used to differentiate interactions of inquilinism, cecidophagy, and kleptoparasitism of galls, as compiled from the literature.

Traits	Inquilinism	Cecidophagy	Kleptoparasitism	Source
Food habit	Exclusively phytophagous	Exclusively phytophagous	Omnivorous habit	Caltagirone 1964; Van Noort et al. 2007; Mound & Morris 2000; Luz et al. 2015
Coexistence with the inducer	Coexistence, if no large tissue modification	Coexistence, but can be lethal	Do not coexist	Sanver & Hawkins 2000; Miyatake et al. 2000; Mound & Morris 2000; Ronquist 1994; Luz et al. 2015
Production of new tissues	Can stimulate production of new tissues when from the same taxonomic group, but when from a different group modifies tissues	Do not modify gall tissue or phenotype	Do not modify gall tissue or phenotype	Brooks & Shorthouse 1997; Ronquist 1994; Van Noort et al. 2007; Sugiura & Yamazaki 2009; Bono 2007; Luz et al. 2015
Phylogenetic relationship with inducer	Close phylogenetic relationship with inducer	No phylogenetic relationship with inducer	Can have a close phylogenetic relationship with inducer	Mani 1964; Sugiura & Yamazaki 2009; Luz et al. 2015
Mobility	Sedentary	High	Low	Stone et al. 2002; Sugiura & Yamazaki 2009; Luz et al. 2015

COEXISTENCE WITH THE INDUCER

Inquilines coexist with the gall inducer when they both feed on the same tissue; e.g., the hymenopteran inquiline *Periclistus pirata* Osten Sacken (Hymenoptera: Cynipidae) on stem galls of *Diplolepis nodulosa* Beutenmüller (Hymenoptera: Cynipidae) (Brooks & Shorthouse 1997). If inquilines do not feed on the same tissues as inducers but modify the tissues, they can be called gall modifiers. Generally, when both organisms belong to the same insect order they are usually non-lethal, but if they are from different taxa, inquilines can become lethal to the inducer, e.g., *Rhoophilus loewi* Mayr (Hymenoptera: Cynipidae) on *Scyrotis* (Lepidoptera: Cecidosidae) galls (Van Noort et al. 2007). On the other hand, cecidophages may coexist with inducers by feeding internally or externally on the gall, and are lethal only when feeding on too much gall tissue, killing the inducer by starvation, or inadvertently opening up the gall. Kleptoparasitism is the only interaction where there is no possibility of coexistence with the inducer (Luz et al. 2015).

PRODUCTION OF NEW TISSUES

The primary characteristic that differentiates inquilinism from the other guilds is their stimulation of the host plant to produce new tissue in galls (Brooks & Shorthouse 1997). This action increases the amount of resources (plant tissue) the gall possesses. This relationship can be beneficial to the inducers (Lászlò & Tóthmérész 2006) when they belong to the same taxon (at least to the level of order). This is because both feed on the nutritive tissue in the same way. If inducers and gall producers of different insect orders encounter one another, their interaction is lethal. Hymenoptera, Diptera, Coleoptera, and Lepidoptera induce the formation of different kinds of gall tissues; inquilines associated with a specific tissue type are compatible with the insect order it belongs to. However, when inquilines occupy galls with incompatible tissue, they modify it. This new tissue then may not be compatible with the initial gall inducer (Van Noort et al. 2007). Moreover, inquilines can also change the shape and color of the gall (Brooks & Shorthouse 1997; Ferraz & Monteiro 2003). This characteristic does not apply to all inquilines but only to those that are gall modifiers. On the other hand, cecidophages and kleptoparasites are incapable of inducing new tissue production or modifying the gall phenotype.

PHYLOGENETIC RELATIONSHIP WITH THE INDUCER

Mani (1964) made the first distinction between inquilines and cecidophages by suggesting that gall tissue feeding inquilines evolved this trait from gall-inducing ancestors, whereas cecidophages evolved the habit of feeding on gall tissue independently. Evidence for this comes from the fact that some inquilines can modify gall tissue and stimulate production of new tissues. Not all inquilines that have a phylogenetic association to the inducer are gall modifiers, as in *Trotteria* (Microthyriaceae: Cecidomyidae) gall producing Cecidomyidae (Gagné 2004). Cecidophages can consume original gall tissue internally, but more commonly externally, differing from inquilines that exclusively consume gall tissue internally.

It is possible also to find inquilines that modify gall tissues that are not phylogenetically closely related to the initiator of the galls they occupy (Van Noort et al. 2007); members of this group belong to the Cynipidae. These hymenopterans have evolved from gall-inducing ancestors with some species attacking inducers other than gallflies (Stone et al. 2002).

Studies by Morris et al. (2000), Bono (2007), and Luz et al. (2015) also have suggested that kleptoparasites may bear a close relationship to inducers because they have the same nutritive tissue compatibility or may have evolved from gall-inducing ancestors (e.g., kleptoparasitc thrips) (Morris et al. 2000). However, more studies must be undertaken to reach a firmer conclusion.

MOBILITY

Inquilines occupy only a single gall where they remain through their immature stage (Stone et al. 2002); cecidophages are more mobile, using 1 or more galls for feeding (Sugiura & Yamazaki 2009), whereas kleptoparasites, though mobile, normally utilize a single gall (Luz et al. 2015).

FINAL CONSIDERATIONS

The major nomenclature problem appears to focus around the term "inquilinism." Historically, all organisms associated with galls that were not predators or parasitoids were placed in this guild (Redfern & Askew 1992). However, it is important to recognize that more than 1 guild that can occupy the "house" of an inducer and must be separated following clear criteria so that biological and evolutionary patterns are not confused.

Moreover, inquilines also have been confused with cecidophages and successors. Nevertheless, successors do not interact with inducers in time, and cecidophages should be considered organisms that may not possess a close phylogenetic association with the inducer, and which are able to feed off more than 1 gall, and are incapable of stimulating new gall tissue production. The largest confusion between inquilines and cecidophages occurs for Coleoptera and Lepidoptera. Probably many of the designated "inquilines" in these 2 orders are actually cecidophages; they do not modify the gall, are not sedentary, and do not have a close phylogenetic relationship with the inducer.

Another problem with the term inquiline can be found in Thysanoptera research. As well-characterized as they are in the literature, the designation of inquilinism in thrips does not fit the broad characterization suggested here. However, we suggest researchers studying Thysanoptera may consider favoring the characterization criteria of inquilinism proposed here, in what seems to us to be a more clearly set of defined terms.

Another important aspect that must be taken into account, primarily by taxonomists that have described cecidogenic species, is that an insect collected directly from a gall may not be an inducer but an inquiline, cecidophage, or a kleptoparasite; this situation can be very common in galls collected from a single sample or period of the yr. Most often these mistakes would involve inquilines, and less frequently cecidophages, because the former are more common and in similar taxa but the latter are mobile.

The inadequate use of the aforementioned terminologies can lead to a poor understanding of interactions in gall-associated guilds. Researchers that work with these systems must take care to distinguish the guilds associated with their components. Unknowingly, many designate all individuals as inquilines, causing great confusion in the literature and erroneous interpretations about the significance of this diversity. In summary, we believe that future research using the criteria suggested in our review could be able to resolve and clarify semantic problems in the specific literature associated with these guilds. It is also anticipated that ecological and evolutionary hypotheses concerning these groups can then emerge with greater clarity.

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