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Size matters: larger galls produced by *Eutreta xanthochaeta* (Diptera: Tephritidae) on *Lippia myriocephala* (Verbenaceae) predict lower rates of parasitic wasps

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Abstract

Gall induction is one of the main life strategies of endophagous insects, which serves to provide food and protection against natural enemies. It is proposed that gall size is one of the most important traits in the life history of the inducer insect, since a balance exists between the protection afforded by the gall and exposure to natural enemies. The aims of this study were first to describe the trophic interactions between *E. xanthochaeta* and its native parasitoids on a new host plant *Lippia myriocephala*, and then to assess the relationships between gall size, location on the plant architecture and parasitism rates. A community of seven native parasitoid morphospecies was found, representing 22.2% of the overall parasitism, highlighting two wasp species, *Torymus* sp. (Torymidae) and Pteromalinae (Pteromalidae) as the most abundant. Gall size exhibited significant variations related to their distribution within the plant architecture, with a gradual reduction in size found from the main stem toward the peripheral branches. Such differences were associated with an increase in parasitized pupae and smaller galls were found to be more susceptible to parasitoid attack. Parasitism rates revealed that *Torymus* sp. uses a broader gall size range than Pteromalinae, and we hypothesized that such variations may be related to certain morphological traits of the parasitoids such as ovipositor length, since the former presents an ovipositor nearly four times longer than the latter. Thus, we infer that growth of bigger galls reduced the likelihood of parasitism of the flies.

Keywords Tri-trophic interactions · Gall size · Parasitism rates · Plant architecture

Introduction

Tri-trophic interactions among plants, insects and natural enemies are a prime component in most terrestrial ecosystems (Schoonhoven et al. 2005). Plant-induced responses can directly affect herbivores by reducing their growth and may also indirectly influence parasitoid performance and host location processes (Poppy 1997; Havill and Raffa 2000). Gall-inducing insects on plants have been used as one of the key references for understanding the dynamics of tri-trophic relationships (Shorthouse et al. 2005). They are highly specialized endophages characterized by inducing some meristematic tissues of their host plants to provide their offspring with food of better nutritional quality and shelter (Fernandes et al. 2014, and references herein). However, galling insects evolved and radiated under heavy parasitoid attack, which may be a selective factor in gall shape, phenology, and position on the plant architecture (Price et al. 1987).

Although the evolutionary patterns driving gall induction as a major life strategy for endophagous insects are unclear, several hypotheses have been proposed concerning the adaptive significance of gall morphology. One of these known as the "enemy hypothesis", proposes that predation rates of gall inducers by natural enemies declines with larger galls, since the structure provides a protective shelter for the

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insect (Price and Clancy 1986; Price et al. 1987; Stone and Schönrogge 2003).

Gall induction has been reported in six insect orders, and the Diptera are outstanding as one of the most important communities, primarily represented by the families Cecidomyiidae and Tephritidae (Freidberg 1997). The latter comprises flies with a range of feeding habits; their endophagous larvae feed on different plant structures, and some taxa have evolved as gall inducers on stems and flowers (Headrick and Goeden 1998). In this context, parasitism by Hymenopteran wasps commonly occurs in diverse genera of Tephritidae, acting to regulate their populations in nature (Hoffmeister 1992; Hoffmeister and Vidal 1994; Freese and Zwölfer 1996; Ovruski et al. 2006). Even though there may be a range of factors that influence parasitism rates, several authors propose that these are associated with certain physical features of galls, such as size, hardness, or the number of chambers inside (Weis et al. 1985; Freese and Zwölfer 1996; Peschken and Derby 1997). These traits are largely influenced by the vigor of the host plant; however, it has been proposed that gall size is a heritable character and an important predictor of survival of the inducer insect, since a trade-off exists between the protection conferred by the gall and exposure to natural enemies (Weis and Abrahamson 1986; Abrahamson and Weis 1997; Stone and Schönrogger 2003). With increased gall size, rates of larval mortality, parasitism, and abortive encapsulation decrease, while those of emergence, weight and fecundity of adults increase (Weis et al. 1983, 1985; Weis and Abrahamson 1985; Romstöck-Völkl 1990).

The impact of parasitism on gall-inducing tephritids has been widely examined, although most studies have focused on the Palearctic and Nearctic species (Turner 1996; Headrick and Goeden 1998). For instance, experimental trials on galls produced by *Eurosta solidaginis* (Fitch) in *Solidago* plants of North America, Wies et al. (1985) discovered that higher parasitism was associated with the wall thickness of galls and the ovipositor length of the parasitoid *Eurytoma gigantea* (Walsh). Studies conducted in Europe on the thistle gall fly, *Urophora cardui* (L.) showed that the increase in cell numbers and gall diameters led to lower larval mortality, providing better protection against parasitoid attack (Freese and Zwölfer 1996). Meanwhile, some Neotropical biocontrol agents as *Procecidochares utilis* Stone and *P. alani* (Steyskal) introduced into Asia to control *Ageratina* species, populations were reduced by native hymenopteran parasites (Julien and Griffiths 1998). In addition, *Cecidochares connexa* (Macquart) was imported into Java and Indonesia for biocontrol of *Chromolaena odorata* (L) King & Robinson (Asteraceae), recording parasitism rates up to 50% by one Eulophidae species in some locations (Cruttwell 1974; McFadyen et al. 2003). Moreover, a survey carried out in South America revealed that flowerhead production of *Vernonia polyanthes* Less. was not adversely affected by stem galls of *Tomoplagia rudolphi* Lutz & Costa Lima but did influence both the host plant architecture and seed viability (Silva et al. 1996).

Eutreta xanthochaeta Aldrich (Diptera: Tephritidae) is a gall-inducing fly of Mesoamerican origin (Mexico and Central America), forming spheroid galls in the stems of *Lantana camara* L. (Verbenaceae), a native weed from the tropical Americas, and actually a major problem as an invasive plant in nearly 60 countries worldwide (Day et al. 2003). Its natural history and interactions with natural enemies have never been studied in its native lands. The single known report from southern Mexico states that this fly induces stem galls in *Lippia substrigosa* Turcz. (Verbenaceae), where it is parasitized by *Opius baderae* Wharton (Hymenoptera: Braconidae) (Wharton and Norrbom 2013). However, parasitism of this fly was investigated in Hawaii, where it was parasitized by non-native Mesoamerican species such as *Diachasmimorpha tryoni* (Cameron), *D. longicaudata* (Ashmead), and *D. kraussii* (Fullaway) (Hymenoptera: Braconidae) (Duan and Messing 1996, 2000; Duan et al. 1996, 1998).

In the state of Veracruz, Mexico, we discovered numerous stem galls in *Lippia myriocephala* Schltdl. & Cham. (Verbenaceae) produced by *E. xanthochaeta*, representing a new native host plant species deserving of investigation, given the significance of this fly brought into other world regions to biocontrol of *Lantana camara*. Therefore, the goals of this study were: (a) describe the trophic interactions of *E. xanthochaeta* with its parasitoids on the newly discovered native host, *L. myriocephala*; (b) characterize the gall distribution in the plant architecture; and (c) assess whether there is a relationship between gall size and parasitism rates by wasps. Our study aimed to identify some adaptive traits produced by these flies under natural conditions, such as gall size and their distribution within the plant architecture, as a response to parasitoid attack.

Materials and methods

Study area

This study was conducted in the central region of Veracruz, Mexico, in a Tropical Montane Cloud Forest or "*Bosque Mesófilo de Montaña*" (BMM), which is recognized as the most diverse ecosystem in Mexico, accounting for 12% of the Mexican flora, with high rates of endemic species (Rzedowski 2006). This ecosystem currently comprises fragmented landscapes, consisting of patches of natural forest and secondary growth species, as result of the establishment of coffee plantations and grasslands (Williams-Linera 2007). Fieldwork was conducted during the dry (March–May 2011 and 2018) and rainy (September–November 2018) seasons in ruderal vegetation, close to pastures and crops in the surroundings of the localities Teocelo (19°23′N, 96° 58´W; 1,160 masl) and Jilotepec (19°37′N, 96° 57′W; 1,252 masl). The weather conditions in both localities are similar, with an average rainfall of 2,000 mm per year, a rainy season from May to October, and dry season from November to April. The average annual temperature is 18 °C, with warmest monthly average in May (27.7 °C), and January the coldest (10 °C) (CONAGUA 2019).

Lippia myriocephala Schltdl. et Cham.

The host plant is a shrub or tree of 1–12 m in height, with leaves of 5–15 cm in length, often with densely spined inflorescences and creamy or white corollas. It grows in the understory on the edges of humid forests, at elevations of 1000–1500 masl. Its native distribution extends from southern Mexico to Panama (Nash and Nee 1984; Vila et al. 2004).

Gall sampling

We surveyed for *E. xanthochaeta* galls on 285 plants of *L. myriocephala* along roads adjacent to coffee plantations and pastures at the two localities. All plants of minimum height 0.80 m were surveyed and measured, gathering all mature galls belonging to the final phases of larval development, characterized by a swelling spheroid shape with evident signs of the development of the fly within.

To determine the gall distribution within the architecture of the plant, two parameters were registered: a) Location, in which the gall was placed into one of four categories: main stem, first branch, second branch, third branch; and b) Position, which was the level of the stem at which the gall was found: basal, medial, or apical (Fig. 1). In the laboratory, we measured the equatorial diameter of each gall (mm). Afterward, the galls were placed individually into plastic breeding chambers of 250 ml and kept under similar conditions of temperature (24 ± 2 °C) and relative humidity (65 ± 12%), with daily observation until emergence of a specimen. Every adult recovered was confirmed to belong in the target species (Stoltzfus 1977), while parasitoids were individually identified using specialized keys (Fernández and Sharkey 2006).

Statistical analyses

To calculate natural parasitism rates, we evaluate the relationship between the number of parasitized pupae and the total number of viable pupae, considered those with emergence of a fly or parasitoid, excluding empty galls, with exit holes, or pupal mortality otherwise than parasitism. Comparisons of the parasitism rates between the dry and rainy seasons were made with a Chi-square test of proportions.

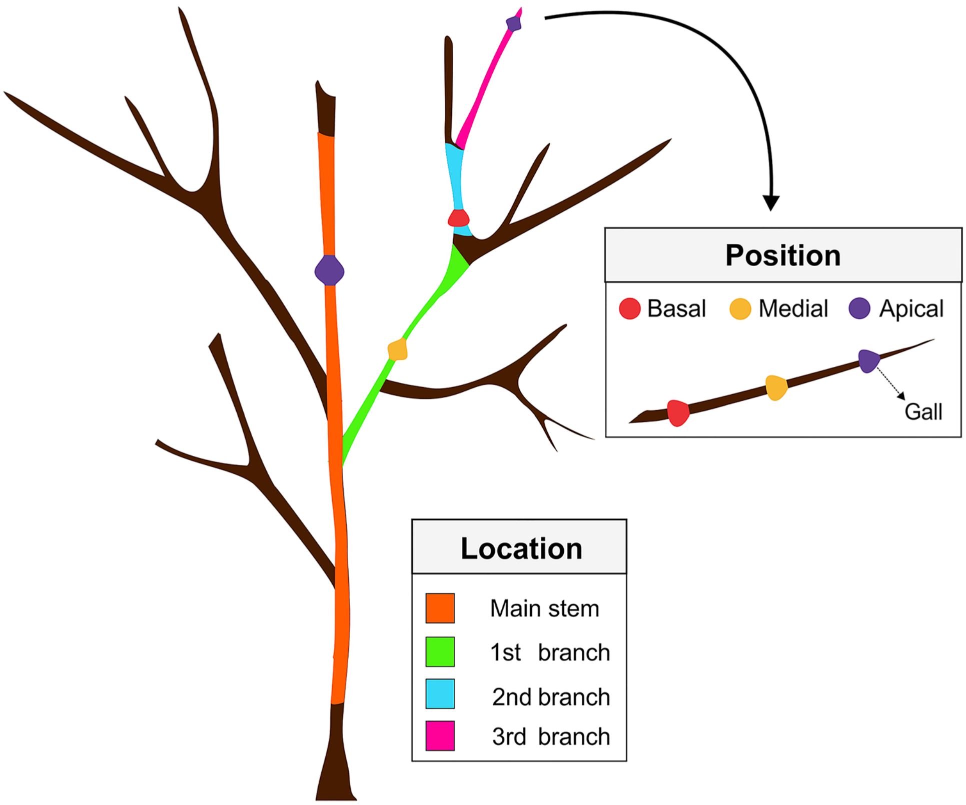

Fig. 1 Schematic of *Lippia myriocephala* illustrating the nomenclature and categories used for location and position of the galls within the plant architecture

A generalized linear model (GLM) with normal distribution was used to test both the size of parasitized and non-parasitized galls and their distribution (location and position) within the architecture of the plant. A logarithmic transformation was applied to the diameter measurements to avoid model overdispersion. Similarly, multiple comparison tests were applied to identify any differences among the categories of the factors under evaluation. Time of emergence was calculated as the period from the date of gall collection to adult emergence and compared through GLM with Poisson distribution. Relationships between gall diameter, parasitism rates and location/position in the plant architecture were analyzed with a GLM with a binomial distribution, assuming occurrence of the parasitoid as a success. The morphological traits of females of the most important parasitoid species were measured, including body length from head to base of the ovipositor, and ovipositor length measured from the base of the second valve to the ovipositor tip. Measurements were compared using a non-parametric Wilcoxon test. All analyses were carried out in the R program version 3.5.1 (R Core Team 2018).

Results

Parasitism rates

A total of 1,217 galls were examined during the study, of which 28.2% (343) were considered as viable pupae, since the others presented adult exit holes, or were occupied by inquilines, or individuals that had died through unknown causes. The parasitoid community of the galls was represented by seven Hymenopteran species in order of importance by the families Torymidae (*Torymus* sp., 13.4%), Pteromalidae (Pteromalinae, 5.2%), in addition to other individuals of Eupelmidae, Braconidae (Opiinae), Encyrtidae (*Aenasius* sp.), Eulophidae and Crabronidae, together scarcely accounting for 3.5% of the parasitized pupae, while the last three exhibited gregarious parasitism (Table 1). From all viable pupae, 267 adults of *E. xanthochaeta* (77.8%) emerged. In addition, there were 76 parasitized pupae (22.2%), some of which had multiple individuals emerging from a single puparium; hence, the fly–parasitoid ratio was 3.5:1.

The times of emergence of adult flies averaged 29.0 ± 8.9 days (mean ± SD), while the parasitoids presented significantly shorter development times at an average of 19.26 ± 11.31 days (mean ± SD), fluctuating between 13.5 and 20.1 days for five of the parasitic species ($X^2_{(0.05;1)} = 160.96$; $p < 0.001$; ISD = 0.58). The galls surveyed displayed a highly fluctuating diameter throughout the entire sample. Adult flies emerged most frequently from the larger galls, with diameter of 15.13 ± 3.7 mm (mean ± SD), ranging from 4.29—26.42 mm. In contrast, the parasitoids emerged from galls that were significantly smaller with diameter of 9.63 ± 4.4 mm (mean ± SD), ranging from 3.56 to 22.80 mm ($F_{(1,342;0.05)} = 145.52$; $p < 0.001$; ISD = 0.05) (Fig. 2).

Most of the parasitic species appeared throughout the dry and rainy seasons, recording 9.8% and 12.2% of the parasitized pupae, respectively, except Encyrtidae, which was only found during the rainy season, while Eulophidae and Crabronidae were only recorded throughout dry season (Table 1). In terms of absolute abundance and sample size, parasitism rates were significantly higher during rainy season ($X^2_{(1,0.05)} = 32.42$, $p < 0.001$). *Torymus* sp. was the dominant parasitoid, exhibiting similar abundances in both seasons (~ 7%), while the Pteromalinae species was scarcely represented during dry season (0.87%), with a significant rise in the rainy season (4.37%).

Table 1 Parasitism rates, emergence times and sexual proportion of *E. xanthochaeta* galls produced on *L. myriocephala* during the dry and rainy seasons in central Veracruz, Mexico

Species	Viable pupae (n)	Emergence (%)			Time of emergence (mean days)	Female	Male	Sexual rate female/male
		Dry season	Rainy season	Total				
Adult flies	267	61.52	16.33	77.8	29.0 ± 8.8	143	124	1.2
Torymidae (*Torymus* sp.)	46	7.00	6.41	13.4	20.1 ± 12.2	31	15	2.1
Pteromalidae (Pteromalinae)	18	0.87	4.37	5.2	17.7 ± 4.9	11	7	1.6
Eupelmidae	6	1.17	0.58	1.8	18.0 ± 15.3	5	1	5.0
Braconidae (Opiinae)	2	0.29	0.29	0.6	22.0**	2	–	–
Encyrtidae (*Aenasius* sp.) *	2 (3)*	0.00	0.58	0.6	13.5 ± 7.8	2	1	2.0
Eulophidae*	1 (8)*	0.29	0.00	0.3	–	8	–	–
Crabronidae*	1 (2)*	0.29	0.00	0.3	1.0**	2	–	–
Totals	343	71.43	28.57	100	–	204	148	

[*] Taxa with gregarious parasitism. Number of specimens recorded in parentheses

[**] Just one observation

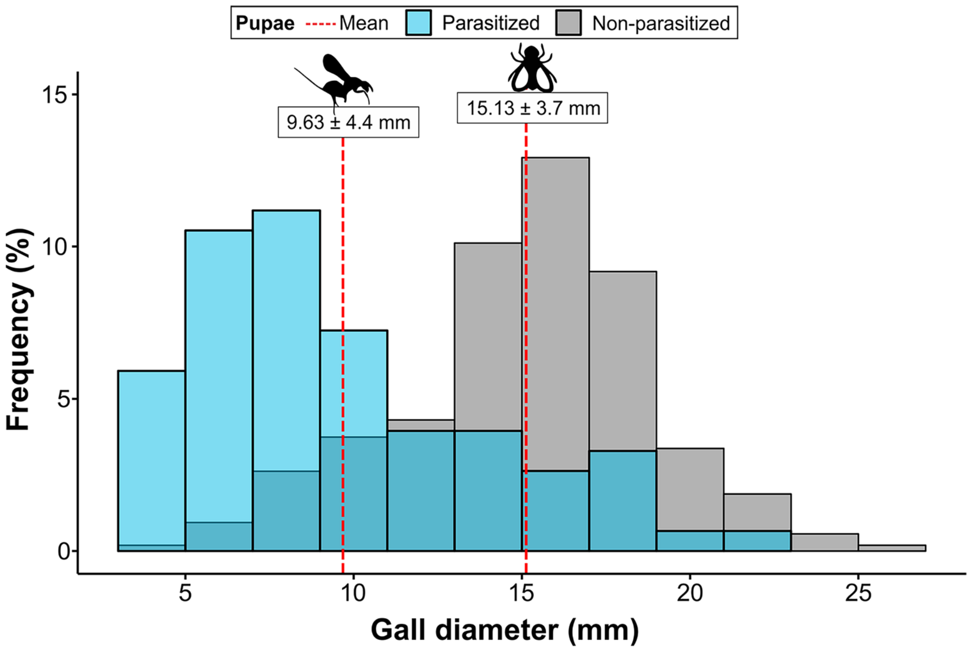

Fig. 2 Analysis of the distribution of gall size and percentage frequency observed for parasitized and non-parasitized galls. Average category sizes show significant differences ($p < 0.001$) using GLM with normal distribution

Gall distribution and plant architecture

Gall size differed significantly depending on location ($F_{(3,326;\ 0.05)} = 13.82$, $p < 0.001$) and position ($F_{(2,326;0.05)} = 13.59$, $p < 0.001$) within the architecture of the plant. Nevertheless, the interaction of these two variables was not directly correlated with gall size ($F_{(6,326;\ 0.05)} = 0.86$, $p = 0.53$). Gall diameter decreased progressively from the main stem toward the periphery of the plant; galls on the main stems were 1.1–1.4 times larger (16.83 ± 3.93 mm, mean ± SD), when compared to those located in first (14.71 ± 4.35 mm), second (12.98 ± 4.30 mm), and third (11.82 ± 4.35 mm) branches.

Gall location was significantly correlated with parasitism rates and gall size ($X^2_{(3;0.05)} = 22.97$; $p < 0.001$; ISD = 0.067), since the galls located on the main stems recorded lower parasitism rates (8.57%), increasing gradually from the first (13.67%), to the second (29.46%) and third (40.38%) branches. According to their position on the branch, both the basal (16.26 ± 3.58 mm) and medial (15.96 ± 4.08 mm) galls became significantly larger than the apical galls (13.18 ± 4.46 mm), although the proportions of parasitism did not differ significantly among the basal (21.43%), medial (15.25%) and apical (24.11%) positions ($X^2_{(2;0.05)} = 1.15$; $p = 0.56$; ISD = 0.003) (Table 2).

Regardless of the location of gall within the plant architecture, both flies and parasitoids emerged from all observed categories, although the former was always more abundant. Based on their branch location, the non-parasitized galls had diameters of up to 1.6 times larger than their parasitized counterparts ($X^2_{(1;0.05)} = 1332.61$; $p < 0.001$) (Fig. 3a); similarly, depending on the position, non-parasitized galls

Table 2 Gall size and parasitism rates based on their location and position within the architecture of *Lippia myriocephala*

Location	Non-parasitized galls	Parasitized galls	Total number of galls	Parasitism rates (%)	Gall diameter (Mean ± SD mm)
Main stem	32	3	35	8.57	16.83 ± 3.93^a
First-branch	120	19	139	13.67	14.71 ± 4.35^b
Second-branch	79	33	112	29.46	12.98 ± 4.30^c
Third-branch	31	21	52	40.38	11.82 ± 4.35^c
Position					
Basal	22	6	28	21.43	16.26 ± 3.58^a
Medial	50	9	59	15.25	15.96 ± 4.08^a
Apical	192	61	253	24.11	13.18 ± 4.46^b

Different letters indicate significant variations among samples ($p < 0.001$)

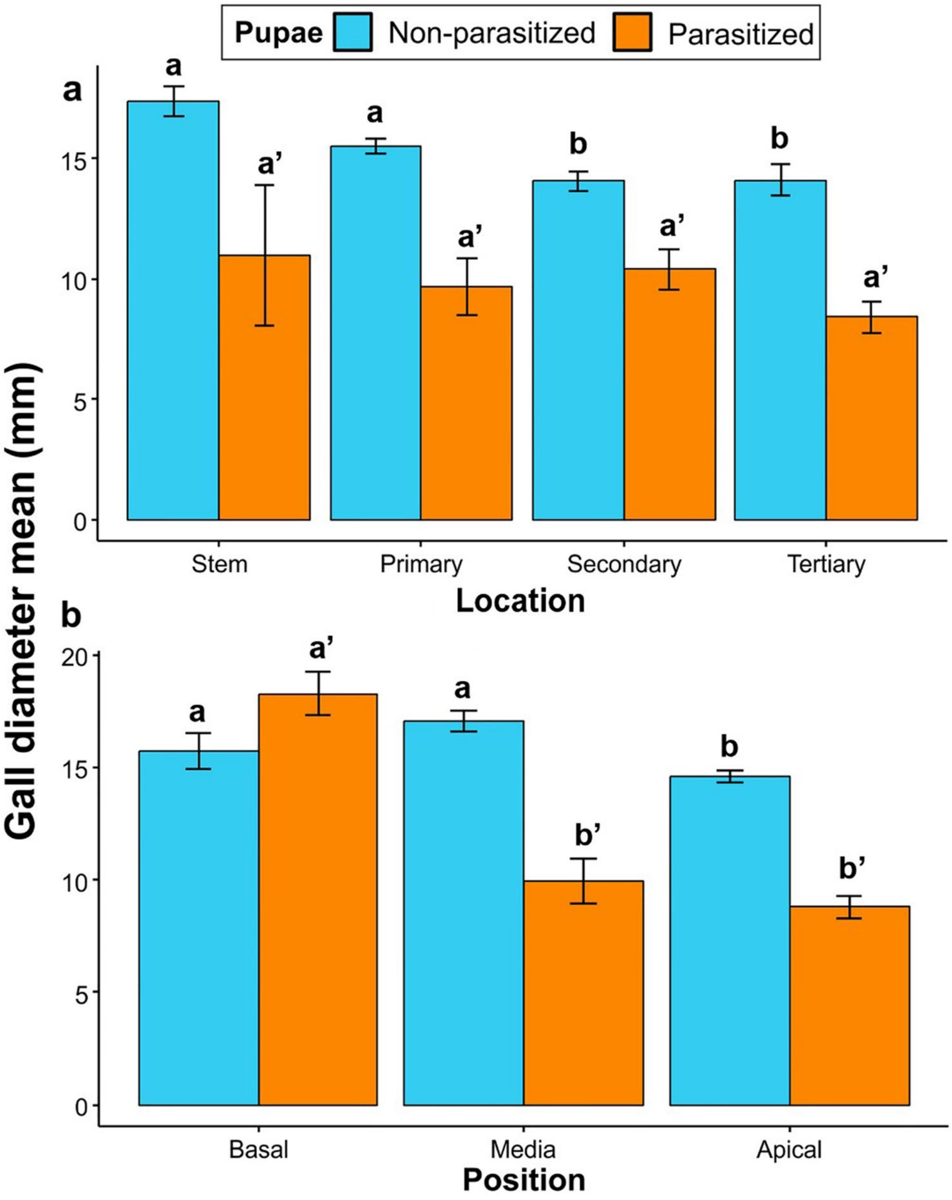

Fig. 3 Gall distribution within the architecture of *Lippia myriocephala* showing the average diameter of parasitized and non-parasitized galls, based on their location (**a**) and position (**b**). In most categories, the non-parasitized galls exhibited larger sizes than those attacked by parasitoids. Different letter indicates highly significant variation ($p < 0.001$) between groups using a multiple comparison test

were up to 1.3 times larger ($X^2_{(1;0.05)} = 1633.11$; $p < 0.001$) (Fig. 3b).

Parasitoid traits

Parasitism rates were inversely correlated to gall size, as the likelihood of parasitism declined with increased gall diameter ($X^2_{(1,0.05)} = 93.47$, $p < 0.001$; ISD = 0.27). Analyses of the independent models for the two major species revealed that *Torymus* sp. had a higher probability of parasitism of 77.8% using galls over a wider size range than Pteromalinae, which exhibited a maximum likelihood of 62.4%. The probability of parasitism by *Torymus* decreased significantly ($p < 0.05$) when galls exceeded 16.01 mm in diameter, whereas in Pteromalinae, that probability declined for galls with diameter greater than 12.78 mm (Fig. 4).

Comparison of female body size showed that *Torymus* sp. is 1.3 times longer (4.31 ± 0.53 mm, median ± IQR) than Pteromalinae (3.27 ± 0.08 mm, median ± IQR), so the ratio between body/ovipositor length was almost 1:1 in the former species, but it was 3:1 in the latter. Furthermore, in absolute terms, the ovipositor length of *Torymus* sp. was 4.27 ± 0.73 mm (median ± IQR), being approximately four times longer than in the Pteromalinae species (1.00 ± 0.27 mm, median ± IQR) (W = 25, $p = 0.007$) (Fig. 5).

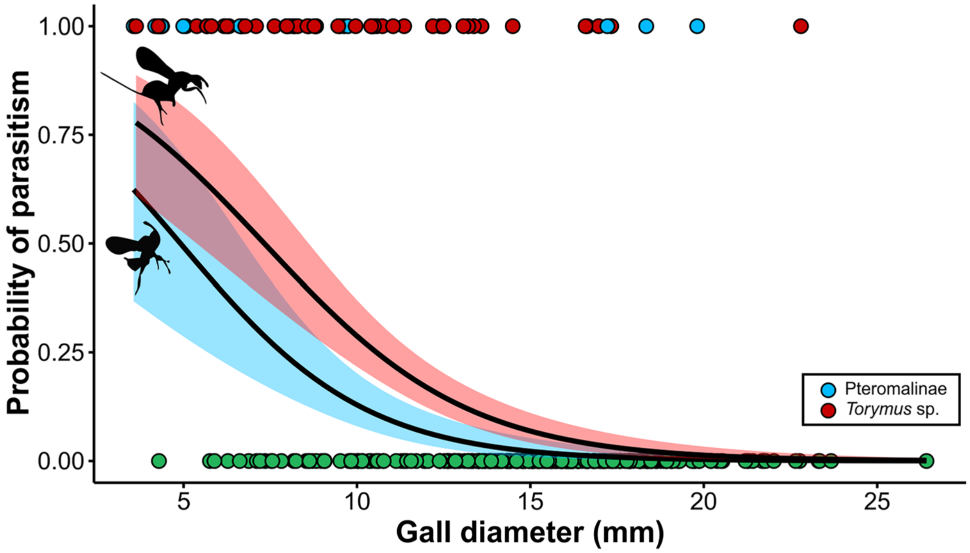

Fig. 4 Probabilistic model between gall size and parasitism rates for two parasitoid wasps, *Torymus* sp. and Pteromalinae. The likelihood of parasitism decreased with increasing gall diameter

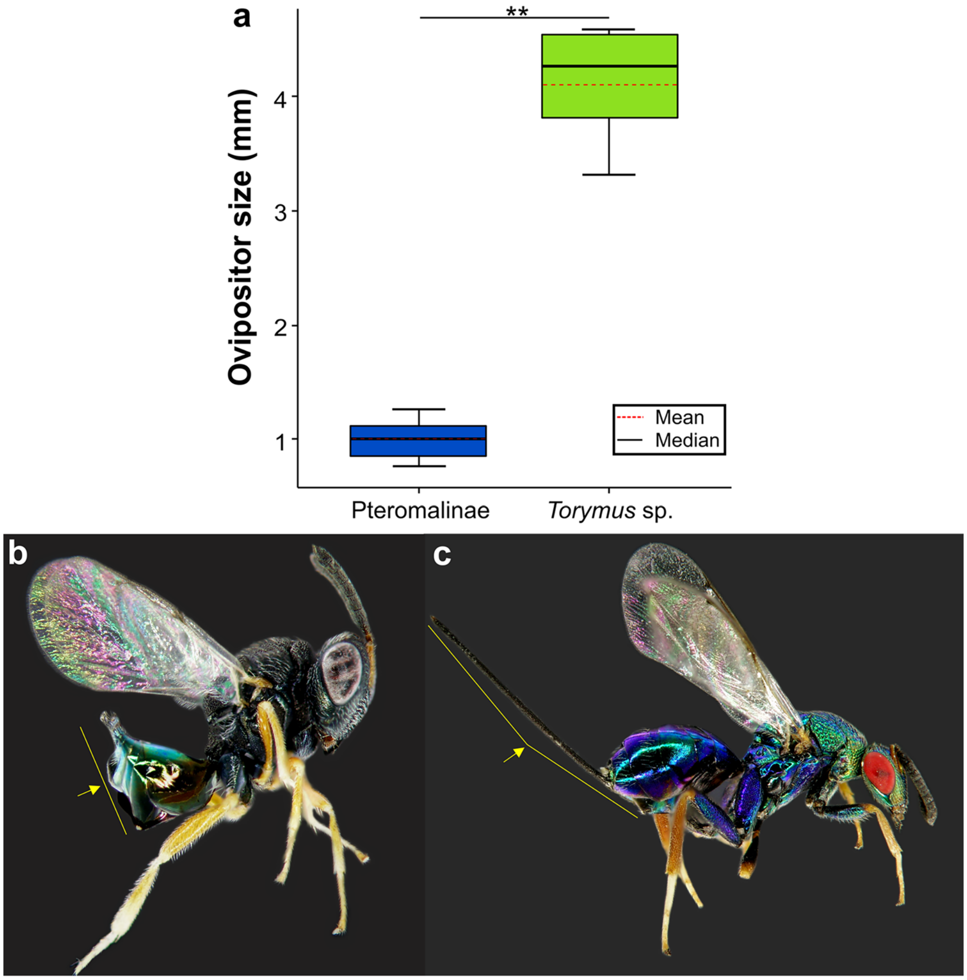

Fig. 5 Analysis of the ovipositor length in the two parasitoid wasps assessed (**a**); females of Pteromalinae (**b**) and *Torymus* sp. (**c**). Asterisk (**) indicates significant differences in the ovipositor length ($p < 0.001$) using a Wilcoxon Test

Discussion

Native parasitoid community

The genus *Eutreta* is native to the Americas, whereas *E. xanthochaeta* is a native species from Mesoamerica feeding on plants of *Lantana camara*. Nevertheless, its biology and related parasitoids have been scarcely investigated in that region. Since 1902, it was introduced to Hawaii coming from Mexico, to be used for biological control of that weed (Aldrich 1923), where later eight Hymenopteran parasitoid species were reported belonging to six families (Braconidae, Eulophidae, Eupelmidae, Eurytomidae, Pteromalidae and Torymidae) (Stoltzfus 1977; Duan et al. 1996, 1997; Duan and Messing 2000). The parasitism rates reported in such cases ranged from 0.1 to 15%, highlighting two Braconid species, *Diachasmimorpha tryoni* and *D. longicaudata,* formerly introduced to Hawaii for the biocontrol of economically significant fruit flies such as *Bactrocera dorsalis* (Hendel) and *Ceratitis capitata* (Wiedemann) (Funasaki et al. 1988).

In Mesoamerica there is a single report of the native parasitic wasp *Opius baderae* Wharton (Hymenoptera: Braconidae) from galls produced in *Lippia substrigosa* (Verbenaceae) (Wharton and Norrbom 2013). As a result of this research, this is the first report of *E. xanthochaeta* using the host plant *L. myriocephala*, together with a rich community of native parasitoids consisting of seven species from six families. In contrast to that reported from Hawaii, our study highlighted two different species with highest parasitism rates, belonging to the families Torymidae (*Torymus* sp.) and Pteromalidae (Pteromalinae), in addition to a low incidence of gregarious parasitism produced by species of Encyrtidae, Eulophidae and Crabronidae. Similarly, in the native North American species *Eutreta diana* (Osten Sacken), a gall-inducing tephritid on the stems of *Artemisia tridentata* Nutt. (Asteraceae), have been reported eight parasitic species from the families Eulophidae (*Euderus* sp.), Eupelmidae (*Eupelmus* sp.), Eurytomidae (4 spp.), Torymidae (*Torymus citripes* Huber) and Pteromalidae (*Lyrcus* sp., formerly *Zatropis* sp.) (Emlen 1992).

The two *Eutreta* species exhibited a highly similar parasitoid community in terms of family richness; however, parasitism rates for *E. diana* (59.7%) were almost 2.7 times higher than those recorded for *E. xanthochaeta* (22.2%). Such differences seem to be related to the ability of produce different gall sizes on their corresponding host plant species; since the galls yielded by *E. diana* ranged from 4 to 14 mm in diameter, while those produced by *E. xanthochaeta* were significantly larger, almost twice as large as the former (3.6–26.4 mm).

Based on our findings, parasitized galls presented a significantly smaller average diameter (9.6 ± 4.4 mm) compared to non-parasitized galls (15.1 ± 3.7 mm), confirming that small galls become highly susceptible to attack by parasitoids. Consequently, it can be inferred that larger galls of *E. xanthochaeta* provide more protection against parasitic attack. This defensive mechanism has also been reported in other gall-inducing tephritid systems (Weis et al. 1985; Price and Clancy 1986; Abrahamson and Weis 1997), but also in several fruit-eating species, where larger fruits presented reduced parasitism rates (Leyva et al. 1991; Hernández-Ortiz et al. 1994; Wang et al. 2009; Sivinski and Aluja 2012).

Parasitism, gall size, and spatial distribution

Some morphological traits of parasitoids could also play an important role in their ability to reach the host larva inside the gall (Weis et al. 1985; Zwölfer and Arnold-Rinehart 1994; Freese and Zwölfer 1996; Duan et al. 1997; Frenzel et al. 2000). In this regard, differences in parasitism rates between the two most abundant wasp species could be attributed to some specific morphological features; firstly, due to the difference in body size, but also the significant differentiation in ovipositor length, since the *Torymus* females possess an ovipositor four times longer than those of Pteromalinae species, a condition that should render the former more able than the latter to reach the host inside the gall. However, foraging strategies are also closely associated with changes in the parasitoid community, with temporary windows of opportunity occurring during gall development (Stone and Schönrogge 2003), which would also play a key role in the reproductive success of the parasitoids. For instance, the interaction of *Eurytoma serratulae* (Fabricius) (Eurytomidae), a specialist parasitoid of the galls of *Urophora cardui* (Linnaeus) (Frenzel et al. 2000), revealed that the short length of the ovipositor of this wasp precluded reaching the host chamber in larger galls, therefore the larvae were parasitized only in the early stages of gall development.

For other gall-inducing insect groups, some authors reported a positive relationship between the complexity of the plant architecture and the richness/abundance of the galls (Fernandes and Negreiros 2001; Araujo et al. 2006; Lara et al. 2008; Clark-Tapia et al. 2013; Boaventura et al. 2018). Our study revealed that the spatial distribution of galls within the host plant architecture was largely concentrated in the first branches, with a progressive decrease toward the periphery of the plant. This pattern is matched by the reduction in gall diameter, which is up to 1.4 times greater on the main stems than on the third branches. The galls occurring in the apical position were the most abundant, but were significantly smaller, suggesting that both factors may be linked to key drivers of natural selection, such as feeding and shelter. The apical meristems are high-quality sites for oviposition since these are active tissues with high nutrient and water concentrations for exploitation by the larva, maximizing their survival and adult reproductive success (Strong et al. 1984; Marquis et al. 2002; Raman 2007).

The gall phenotype is influenced both by the genotypic expression of the inducing insect and its host plant; in turn, it could depend on the selective pressures exerted by the two interacting species, and the heritability of the phenotype (Weis and Abrahamson 1986). It has been reported that some morphological features of the branches, such as diameter or weight, could restrict the growth of galls (Mani 1964). For instance, Weis and Kapelinski (1984) found a positive correlation between size of galls produced by *Rhabdophaga strobiloides* Osten Sacken (Diptera: Cecidomyiidae) and branch diameter in *Salix cordata* Michx. (Salicaceae). That study suggests that the thickness of the branches chosen by females of *E. xanthochaeta* determines the potential gall size according to their location within the plant architecture.

Weis and Abrahamson (1986) proved that gall size variation in *E. solidaginis* resulted from intraspecific genetic variation, despite selective pressures by natural enemies. However, larvae that produced smaller galls were largely parasitized, while those of larger size showed greater propensity to bird predation. The balance of these opposite selective forces favored phenotypes with medium-sized galls. Therefore, our findings suggest that flies demand the development of bigger galls to reduce the probability to be parasitized, and these structures are concentrated in the central part of plant architecture where the nutrients required by the larva are probably unavailable in the same quality and quantity. The two-way interaction of both factors leads to a trade-off between thinner branches with higher nutrient contents, and thicker branches with lower nutrient contents where bigger galls can be developed, protecting the larvae from the attack of parasitoids. This acts to promote the selection of intermediate-sized galls, located on the first and second branches.

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Authors' contributions The study conception and design were made by VH-O and MH-L. Material preparation, data collection and analysis were performed by MH-L and VH-O. The first draft of the manuscript was written by MH-L and VH-O; and GWF and GC-C commented, review and editing on previous versions of the manuscript. All authors read and approved the final manuscript.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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