Arthropod-Plant Interactions (2022) 16:631–643
https://doi.org/10.1007/s11829-022-09927-8

ORIGINAL PAPER

Quantitative trophic networks of insect gallers and their parasitoids in the hybrid oak complex *Quercus magnoliifolia* x *Quercus resinosa*

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Received: 26 October 2021 / Accepted: 19 September 2022 / Published online: 6 October 2022
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Abstract

Oak hybridization have important effects on the structure of herbivorous insect communities and associated natural enemies. We tested the effects of hybridization between *Q. magnoliifolia* and *Q. resinosa* on insect gallers trophic networks and their parasitoids. We characterized the genotypes of 35 individuals of *Q. magnoliifolia*, 30 of *Q. resinosa*, and 57 hybrids using eight nuclear microsatellite markers. We collected 6,798 galls from the oak hybrid complex distributed in 33 gall morphospecies on *Q. magnoliifolia,* 28 on *Q. resinosa,* and 42 on hybrid oaks. Galler-parasitoid networks were realized by 21 gall morphospecies and 21 parasitoid species for *Q. magnoliifolia*; 16 gall morphospecies and 30 parasitoid species for *Q. resinosa*; and 25 gall morphospecies and 23 parasitoid species for hybrids. Plant-galler networks were different among three oak groups, having the hybrid network higher values of diversity of interactions, nestedness and modularity and lower values of specialization than *Q. magnoliifolia* and *Q. resinosa* networks. Hybrid network of gallers and parasitoids had higher diversity of interactions, connectance and generality and lower modularity than *Q. magnoliifolia* and *Q. resinosa* networks. Hybrids are more vulnerable to insect galler incidence having low pressure by parasitoids, which allow more gall incidence in hybrid plants. Our study corroborated that hybridization generates changes in oak genetic composition influencing insect gallers trophic networks and their parasitoids. Our findings are also consistent with the rule of genetic similarity which suggest a relationship between plant genetics and the associated arthropod community, where genetically similar plants support similar arthropod communities.

Keywords Gallers · Herbivore-parasitoid interactions · Hybrid complex · Trophic networks · Oaks · Parasitoids

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Handling Editor: Makoto Tokuda.

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Introduction

Understanding the mechanisms that determine community organization is one of the main goals of ecology (Loreau et al. 2001; Cronin et al. 2020). Ecological interactions constitute one of these mechanisms, since the nature of species interactions and their persistence in time and space shape the structure and stability of communities (Elsadany et al. 2012; Fagundes et al. 2018). Species interactions can be represented as complex ecological networks, in which each species generally interacts with other species within and between trophic levels (Waser and Ollerton 2006; Tylianakis and Morris 2017). Therefore, ecological network theory provides an approach to understand multi-species interactions in complex systems by representing species as nodes and interactions as linkages, and then estimating different network metrics (Jordano et al. 2009).

During the last two decades, this approach has allowed a considerable increase in our understanding of the patterns related to the organization and stability of natural communities (Tylianakis and Morris 2017; Landi et al. 2018). Because quantitative trophic networks incorporate information about the frequency and abundance of interactions (Alhmedi et al. 2011), they provide a clear functional description of community structure (Delmas et al. 2019; Oliveira et al. 2019). Most studies of trophic networks have focused on mutualistic interactions, mainly pollination (Welti and Joern 2015; Losapio et al. 2019), seed dispersal (Donatti et al. 2011; Sebastian-Gonzalez et al. 2015), as well as mutualisms between plant and ants (Rico-Gray et al. 2012; Staab et al. 2017). However, fewer studies of trophic networks have focused on antagonistic interactions (Kaartinen and Roslin 2012; Oliveira et al. 2019). For example, recent evidences indicate that intraspecific genetic variation can affect the topology of trophic networks (Barbour et al. 2016), but little is known about the effects of plant hybridization on the structure of the trophic network of associated insects, especially those that include three trophic levels (Lau et al. 2016; Keith et al. 2017).

Hybridization is a natural phenomenon defined as the successful mating between individuals belonging to populations that differ in at least one heritable character (Martinsen et al. 2001). Hybridization frequently occurs in many plant groups and is considered an important evolutionary mechanism with a suite of possible outcomes, including the transference of adaptive variation between species and the production of novel adaptations (Carson and Dowling 2006; Cheng et al. 2011), and the modification of genetic variation and diversification patterns (Soltis and Soltis 2009). Plant hybridization can also have important consequences for associated organisms, since genetic differences among parental plant species and hybrids can determine variation in the composition and structure of their insect herbivore community, mutualists, predators and parasitoids (Lau et al. 2016; Pérez-López et al. 2016; Maldonado-López et al. 2018). For example, some studies show that intraspecific genetic variation in multiple plant traits can be related to variation in the community structure of diverse organisms, from microbes to vertebrates (Whitham et al. 2012; Keith et al. 2017). Therefore, trophic networks can provide a useful approach to quantify the consequences of plant hybridization on the community of associated insect herbivores and their natural enemies.

The genus *Quercus* (Fagaceae) is a highly diverse group of woody plants with temperate origin known for a high frequency of interspecific hybridization (González-Rodríguez et al. 2004; Cavender-Bares and Pahlich 2009). The genus includes 300–600 species distributed throughout the northern hemisphere (Jones 1986). Mexico is a main center of diversification with approximately 161 species, 109 of which are endemic (Valencia 2004; Hipp et al. 2018). Oak species harbor a great diversity of insect herbivores (Stone et al. 2002; Maldonado-López et al. 2018), including cynipid gall wasps (Hymenoptera: Cynipidae) (Pérez-López et al. 2016). More than 80% of the approximately 1000 species of cynipid gall wasps are associated with oak species (Stone et al. 2002). A recent multiple-taxonomic comparison of plant-galler interactions showed that cynipids are involved in complex networks of interactions with their host plants, with many species occurring over different species of oak trees (Araújo et al. 2019).

Gall induction represents a complex developmental process resulting from a stimulation of injected fluids by female wasps during oviposition, or by secretions of saliva by larvae during feeding (Dreger-Jauffret 1992). This chemical interaction generates hypertrophy (i.e., abnormal growth of cells) and hyperplasia (i.e., abnormal multiplication of cells) that lead to the abnormal structures of plant tissues called galls, where wasp insects spend most of their life cycle (Stone and Schönrogge 2003). Each wasp species induces a particular and distinct gall morphology, which is mainly controlled by the insect (Maldonado-López et al. 2016; Pérez-López et al. 2016; Coutinho et al. 2019). In general, cynipid gall wasps are highly specific to their host plants and can discriminate between closely related hosts (Evans et al. 2012). Besides, some studies have reported the presence of super hosts (i.e., plants that support several gall-inducing species) as result of historical and ecological traits (e.g., wide geographical distribution) (Mendonça 2007; Fagundes et al. 2020). Phylogenetic proximity and consequently genetic, phytochemical, and morphological similarity may lead some species of insect gallers to be able to use closely related host plant species (Coutinho et al. 2019). In the case of the cynipid-oak system, there is evidence that cynipid galler wasp species are able to colonize different host species (Araújo et al. 2019). These results lead to the expectation that hybridization in oaks may be an important factor to increase the sharing of cynipid gall wasps between species, as well as to enhance the colonization of insect gallers in new oak hosts.

On the other hand, natural enemies such as predators and parasitoids cause high mortality on cynipid gall wasp species associated with oak species (Schönrogge et al. 2006; Chust et al. 2007) acting as top-down forces regulating the structure of the cynipid community (Cooper and Rieske 2010). Particularly, parasitoids of cynipids (i.e., families Ichneumonidae, Braconidae, and Chalcidoidea) are responsible for 40–100% of mortality of cynipids in natural communities (Stone et al. 2002; Hayward and Stone 2005) and vary in their host specificity, with a large number of polyphagous species and a limited number of specialist parasitoids (Askew 1984). Some studies suggest that both specialist and generalist parasitoids differentially influence food webs (Schönrogge and Crawley 2000; Stone et al. 2002). In fact, specialist parasitoids have little influence on trophic webs because they attack few insect galler species, while generalist parasitoids can have larger effects as a result of both killing insect gallers and generating competition with other parasitoid species (Bailey et al. 2009, Lepais and Gerber 2011). Parasitoids of cynipid gall wasps and gall midges are also divided into early attacker and late attacker, based on the ontogenetic moment they colonize galls (Stone et al. 2002). However, little is known about tri-trophic interactions that include plants, galls, and parasitoids in temperate ecosystems, and even less in hybrid oak complexes.

In Mexico, the formation of hybrid zones between *Quercus* species with different degrees of relatedness (Pérez-López et al. 2016; Cuevas-Reyes et al. 2018; Maldonado-López et al. 2018) offers an excellent opportunity to analyze the effects of host-plant genetic variation on the trophic webs in natural communities. Therefore, the goal of this study was to examine the effects of hybridization in a complex of two Mexican white oaks, *Q. magnoliifolia* and *Q. resinosa* on the trophic networks of cynipid gall wasps and their parasitoids at a local scale in the Tequila Volcano, Mexico. We describe the structure of trophic networks using network measures of species diversity (number of species at upper and lower trophic level) and interactions (diversity of interactions, connectance, specialization, generality, and vulnerability) and arrangement of interactions (modularity and nestedness). The specific questions addressed were as follows: (i) Does the structure of trophic networks of cynipid gall wasps and their parasitoids differ between parental and hybrid plants in the hybrid oak complex *Quercus magnoliifolia* x *Quercus resinosa*? (ii) Does the specificity of parasitoids to cynipid gall wasp species differs in the trophic networks of parental and hybrid plants? We expect that due to the sharing of species and interactions between parental plants, hybrid individuals should form a network more diverse in species and interactions and less specialized (i.e., more connected, less modular, and more nested) than the networks of *Quercus magnoliifolia* and *Quercus resinosa* plants. Similarly, we hypothesized that the specificity of the parasitoids must be greater in the networks of parental plants than in the network of hybrid oaks.

Materials and methods

Study system

This study was conducted at the Tequila volcano, Jalisco state, Mexico (20°50’ N, 103°5’ W). In this volcano, *Quercus magnoliifolia* occurs between 1400 and 1800 m a.s.l. (Pérez-López et al. 2016). This is a tree which can reach up to 25 m in height, with obovate leaves, lustrous and almost glabrous on the adaxial surface, while the abaxial surface is tomentose with glabrescent petioles (Arizaga et al. 2009). *Quercus resinosa* is a tree growing up to 10 m and it is distributed from 1700 to 2100 m of elevation (Pérez-López et al. 2016). The leaf shape is obovate, rugose on the adaxial surface, and tomentose on the abaxial surface (Arizaga et al. 2009). A hybrid zone has been reported previously to occur between these two oak species, with hybrids being present at the whole altitudinal gradient but being more abundant between 1600 and 1800 m (Albarrán-Lara et al. 2010, 2019; Pérez-López et al. 2016). Previous morphometric analyses have shown that the two species are clearly differentiated and that hybrid individuals have an overall intermediate leaf shape (Albarrán-Lara et al., 2010; 2019).

Sampling design

Galls were collected from 50 individuals of the *Q. magnoliifolia* x *Q. resinosa* complex located between 1400 and 1500 m a.s.l. at the Tequila Volcano, 50 individuals between 1600 and 1800 m, and 50 individuals between 1900 and 2100 m. At each of these altitudinal intervals, *Q. magnoliifolia*, hybrids, and *Q. resinosa* trees are, respectively, more abundant (Albarrán-Lara et al. 2010; Pérez-López et al. 2016). The genetic assignment of each individual tree into genotypic classes (i.e., pure parental of the two species and hybrids) was performed using eight nuclear microsatellites that previously have been shown to have enough discriminatory power (see Albarrán-Lara et al. 2010; Pérez-López et al. 2016).

To collect galls, a systematic stratified sampling design was used by collecting three branches of similar length at each level of the crown of each tree: lower, medium, and upper (Maldonado-López et al. 2015). Each individual tree was permanently marked with aluminum tags. Samplings were performed monthly from July to February in two consecutive years (2011–2012 and 2012–2013). In each sampling year, we collected different branches from each tree marked of the *Q. magnoliifolia* x *Q. resinosa* complex. Cynipid species display alternation of generations in the same year, where the sexual generation occurs in the spring and the asexual generation in the summer and autumn (Stone et al. 2002; Maldonado-López et al. 2016). In the Tequila volcano, the dry season where the oaks lose their leaves is from March to June (i.e., spring), while the oaks maintain their leaves during July to February (i.e., summer and autumn) (Hernández-Calderón et al. 2013). Therefore, our sampling only included the asexual generation of the cynipid galls. In the field, all leaf and branch galls were separated and placed in plastic containers covered with tulle mesh and transported to the laboratory to wait for the emergence of the adult gall inducers and parasitoids. In the laboratory, leaf and branch galls were reared independently at a temperature of 20–23 °C in plastic cups covered with microfabric to allow air circulation. The insects that emerged from the galls were stored in 70% alcohol for taxonomic identification (i.e., parasitoid insects) using the taxonomic keys of Graham (1969), Borror et al. (1976), Graham and Gijswijt (1998 and Gibson et al. (1997). Galls were assigned to morphospecies according to their external morphology (Gagné 1994; Pérez-López et al. 2016). The use of morphospecies is a reliable approach to estimate the diversity and structure of insect galler communities, since usually each species of insect induces a gall with a unique morphology (Araújo et al. 2013; Pérez-López et al. 2016). However, whenever possible, the adult insect gallers were kept in ethanol as vouchers.

Comparing communities of insect gallers and parasitoid cynipids between oaks

To test for differences in communities of insect gallers and cynipid parasitoids among the three groups of oaks (*Q. resinosa*, *Q. magnoliifolia*, and hybrids), we performed a Non-Parametric Multivariate Analysis of Variance (NPMANOVA) based on an abundance matrix of insect gallers and parasitoids found in oaks. In addition, we estimated the Jaccard similarity index, using the EstimateSWin820 program (Colwell 2009), to compare the similarity of species composition between the three oak categories for both insect gallers and parasitoids. The richness of the parasitoid species present in each of the three oak groups with galls was obtained by rarefaction curves using the program EstimateS 9.1.0 (Colwell 2013). Because the number of plants with galls in the three oak groups was different, the richness species value was standardized (Gotelli and Colwell 2001). The scale of the independent variable (X) was represented by the accumulated number of plants with galls.

Trophic networks

Quantitative trophic networks (based on abundance) were constructed for the three oak groups (*Q. magnoliifolia*, *Q. resinosa*, and hybrids) according to the genetic assignment analysis as the first trophic level, insect galler species as the second trophic level, and the parasitoid species as the third trophic level. Metrics describing the topology of the networks were calculated for each genotypic class (*Q. magnoliifolia*, *Q. resinosa*, and hybrids) in two bipartite networks. The first network analyzed the interactions among the individuals in each oak genotypic class with gall morphospecies, and the second network analyzed the interactions among the gall morphospecies and parasitoids. Interactions in the bipartite networks were quantified considering the total abundance of gall morphospecies and their parasitoids in the community, respectively.

To characterize the trophic structure of the networks, we used the following network descriptors: diversity, connectance, specialization, vulnerability, generality, modularity, and nestedness. We calculated the diversity index of interactions based on the Shannon index (Kaartinen and Roslin 2012). Connectance was calculated as the proportion of possible interactions that are realized in the network (Dormann et al. 2009). Network specialization was obtained using the index H_2, which can take values from 0 (absolute generalization) to 1 (absolute specialization). To determine the average number of oak categories attacked (i.e., parental plants and hybrid plants) by each insect galler species and the average number of gall morphospecies attacked by each parasitoid species, we used the generality metric (Jordano 1987). Similarly, to evaluate the average number of insect gallers that attack each oak individual and the average number of parasitoids that attack each gall morphospecies, we used the vulnerability measure (Jordano, 1987). We calculated the modularity index in order to identify, within a trophic network, the presence of species groups/modules of a particular trophic level that interact more frequently with another group of species from another trophic level (Marquitti et al. 2014). This index takes values from 0 to 1, with higher values indicating the existence of modules or semi-independent sets of interactors within the general network (Dormann et al. 2009). In each subnetwork, the distribution of species interactions was determined by calculating the nesting index using the NODF metric based on overlap and decreasing fill (Almeida-Neto et al. 2008) that identifies the species with the highest number of interactions at each trophic level (i.e., hyper-connected species, generalist-generalist, generalist-specialist and specialist-specialist interactions) (Almeida-Neto et al. 2008).

In order to test the significance of network descriptors obtained for the different bipartite networks we used 500 simulated networks generated by null models (Dormann and

Strauss 2014). Null models were generated using the quasiswap algorithm (Dormann et al. 2009). All network analyses were performed in the BIPARTITE package (Dormann et al. 2008) on R software (ver. 2.8.1). Visual representations of network structure were constructed with Pajek 3.10 (Batagelj and Mrvar 1998).

Finally, in each network, the species were categorized as generalist species nucleus (i.e., generalist species with many interactions) and peripheral species (i.e., selective species with few interactions) to assess the replacement of species between the insect gallers and parasitoids within each subnetwork in each host oak category (Dáttilo et al. 2014).

Results

General results

According to the genetic analyses, 35 oak individuals were assigned to *Q. magnoliifolia*, 30 to *Q. resinosa*, and 57 were genetically intermediate (hybrids) (see Pérez-López et al. 2016). We had failures in the amplification of some microsatellite loci of 28 of the oak individuals collected that were therefore not assigned to a category.

In total, we collected 6,798 cynipid galls from the hybrid complex *Q. magnoliifolia* x *Q. resinosa*. Of these, we identified a total of 33 gall morphospecies on *Q. magnoliifolia*, 28 on *Q. resinosa*, and 42 on hybrid oaks. Additionally, we reared over 2700 parasitoids belonging to 45 different species, 19 genera and seven families (Eurytomidae, Eulophidae, Ormyridae, Torymidae, Pteromalidae, Eupelmidae, and Encyrtidae).

We found a total of 20 parasitoid species associated with galls of *Q. magnoliifolia*, 30 with galls of *Q. resinosa*, and 22 with galls of hybrids oaks. The rarefaction curve suggested that we reached a high level of completeness with a standard sample size of 30 plants. Moreover, the rarefaction curves also suggested that the richness of gall parasitoid species was higher in *Q. resinosa* than in hybrids and *Q. magnoliifolia* (Fig. 1).

The results of NPMANOVA indicated that communities of insect gallers change among oaks plants ($F = 3.645$, $P < 0.001$), with the post hoc pairwise comparisons showing that insect galler communities varied significantly among all oak categories ($P < 0.05$). The communities of insect galler parasitoids also change among oak categories ($F = 4.1$, $P < 0.001$). However, results of post hoc pairwise NPMANOVA showed that the communities of insect gallers varied significantly only between *Q. magnoliifolia* and *Q. resinosa* ($P < 0.001$), and between hybrids oaks and *Q. resinosa* ($P = 0.007$).

The Jaccard similarity index showed that *Q. resinosa* individuals had a greater similarity of insect galler species (51%) and parasitoids (56%) with the hybrids. While the *Q. magnoliifolia* individuals had a similarity of 46% in insect galler species and 36% in parasitoid species with the hybrids. The similarity in the composition of insect galler species and parasitoids between *Q. magnoliifolia* and *Q. resinosa* were 19% and 50%, respectively.

Plant–insect galler networks

The plant–insect galler networks were composed by 35 oak individuals and 33 insect galler species for *Q. magnoliifolia*, 30 oaks individuals and 28 insect galler species for *Q. resinosa* and 57 oak individuals and 42 insect galler species for hybrids. The network of *Q. magnoliifolia* had five exclusive species of insect gallers (15.2%), while *Q. resinosa* registered only one exclusive insect galler

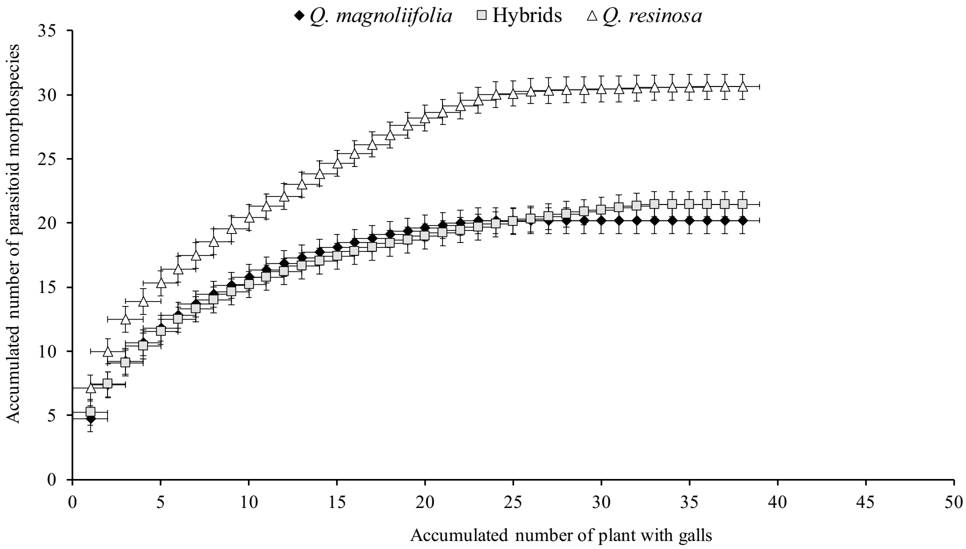

Fig. 1 Rarefaction curves showing the accumulated number of plants with galls and the accumulated number of parasitoid morphospecies. Diamonds *Q. magnoliifolia*, triangles *Q. resinosa*, and boxes hybrids

species (3.6%). For hybrid oaks there were seven exclusive insect galler species (16.6%).

Topological descriptors ranged greatly between *Q. magnoliifolia*, *Q. resinosa*, and hybrid networks (Table 1). The hybrid network had the highest diversity of interactions (5.583) when compared to the *Q. magnoliifolia* (5.021) and *Q. resinosa* (4.457) networks. Similarly, the hybrid network was more nested (30.468) than the *Q. magnoliifolia* (26.636) and *Q. resinosa* (29.159) networks. Network modularity also was higher for the hybrid network (0.510) than for the other two networks (0.372 and 0.429 for *Q. magnoliifolia* and *Q. resinosa* networks, respectively). On the other hand, specialization was lower for the hybrid network (0.000) than for the other networks (*Q. magnoliifolia* = 0.466 and *Q. resinosa* = 0.438). The connectance was higher for the *Q. resinosa* (16.4%) than for the *Q. magnoliifolia* (14.5%) and the hybrid (10.8%) networks. Both generality and vulnerability were higher for the hybrid network (14.879 and 7.045, respectively) than for the networks of *Q. magnoliifolia* (9.576 and 5.932, respectively) and *Q.* resinosa (7.080 and 4.778, respectively).

Null model comparisons showed that the observed values of diversity of interactions, connectance, nestedness, modularity, generality, and vulnerability of the oak hybrids network were higher than expected by chance (Table 1). On the other hand, the hybrid network had a lower value of specialization than expected by null models. For both *magnoliifolia* and *Q. resinosa* networks, null model values indicated less diverse, connected, nested, modular, general and vulnerable networks than expected by chance. The networks of the two parental oak species had higher modularity and specialization than null model expectation.

Insect galler-parasitoid networks

Interactions of insect gallers and parasitoids were realized by 21 gall morphospecies and 21 parasitoid species (with four exclusive parasitoid species = 19.0%) for *Q. magnoliifolia*; 25 insect gallers species and 23 parasitoid species (six exclusive parasitoids = 26.0%) for hybrids, and 16 insect gallers species and 30 parasitoid species (10 exclusive = 33.3%) for *Q. resinosa*.

The *insect galler-parasitoid* network of *Q. magnoliifolia* was structured by a nucleus of 11 generalist species of insect gallers (33.3%) that were interconnected with more than three different parasitoid species, and eight peripheral insect galler species that were parasitized by only one parasitoid species (24.0%) (Fig. 2). Of this generalist species nucleus of insect galler species, four were shared with the networks of hybrids and *Q. resinosa* (see Fig. 2, 3, 4). In the network of *Q. resinosa*, we detected six nucleus generalist insect galler species that were parasitized by at least three different parasitoid species (20.0%) (Fig. 3). We also observed 11 nucleus species of parasitoids (36.7%), eight peripheral parasitoid species that parasitized only one insect galler species (26.6%), and three parasitoid species associated with two insect galler species (10.0%) on Q. *resinosa* oaks (Fig. 3). For hybrid oaks, we detected 10 nucleus generalist species of galler insect species that were parasitized by at least three different parasitoid species (23.8%) (Fig. 4). We also observed 10 nucleus species of parasitoids (43.4%), eight peripheral parasitoid species that parasitized only one insect galler species (34.8%), and three parasitoid species associated with two insect galler species (13.0%) (Fig. 4).

Insect galler-parasitoid networks of *Q. magnoliifolia*, *Q. resinosa*, and hybrid oaks differed in the network descriptors (Table 2). The hybrid network had higher diversity (0.136), connectance (13.6%), and generality (5.855) than *Q. magnoliifolia* (3.324, 10.4%, and 3.315,

Table 1 Descriptors of the plant–insect galler networks of *Q. magnoliifolia*, hybrids, and *Q. resinosa* individuals

Network descriptor	*Q. magnoliifolia*		Hybrids		*Q. resinosa*	
	Observed	Null models	Observed	Null models	Observed	Null models
Nsp-UTL	33	–	42	–	28	–
NInd-LTL	35	–	57	–	30	–
Diversity of interactions	5.021	6.061 (±0.006)	5.583	5.381 (±0.026)	4.457	5.533 (±0.005)
Connectance	0.145	0.500 (±0.005)	0.108	0.093 (±0.001)	0.164	0.594 (±0.008)
Nestedness	26.636	76.286 (±1.176)	30.468	22.213 (±1.401)	29.159	81.990 (±1.421)
Modularity	0.372	0.087 (±0.004)	0.510	0.099 (±0.004)	0.429	0.073 (±0.004)
Generality	9.576	24.405 (±4.588)	14.879	11.287 (±2.917)	7.080	16.998 (±1.970)
Vulnerability	5.932	15.157 (±4.589)	7.045	5.587 (±2.818)	4.778	13.145 (±1.974)
Specialization	0.438	0.055 (±0.002)	0.000	0.116 (±0.14)	0.466	0.040 (±0.002)

Number of species at the upper trophic level (Nsp-UTL). Number of individuals at the lower trophic level (NSp-LTL). All observed values were significantly different of null models ($P < 0.05$)

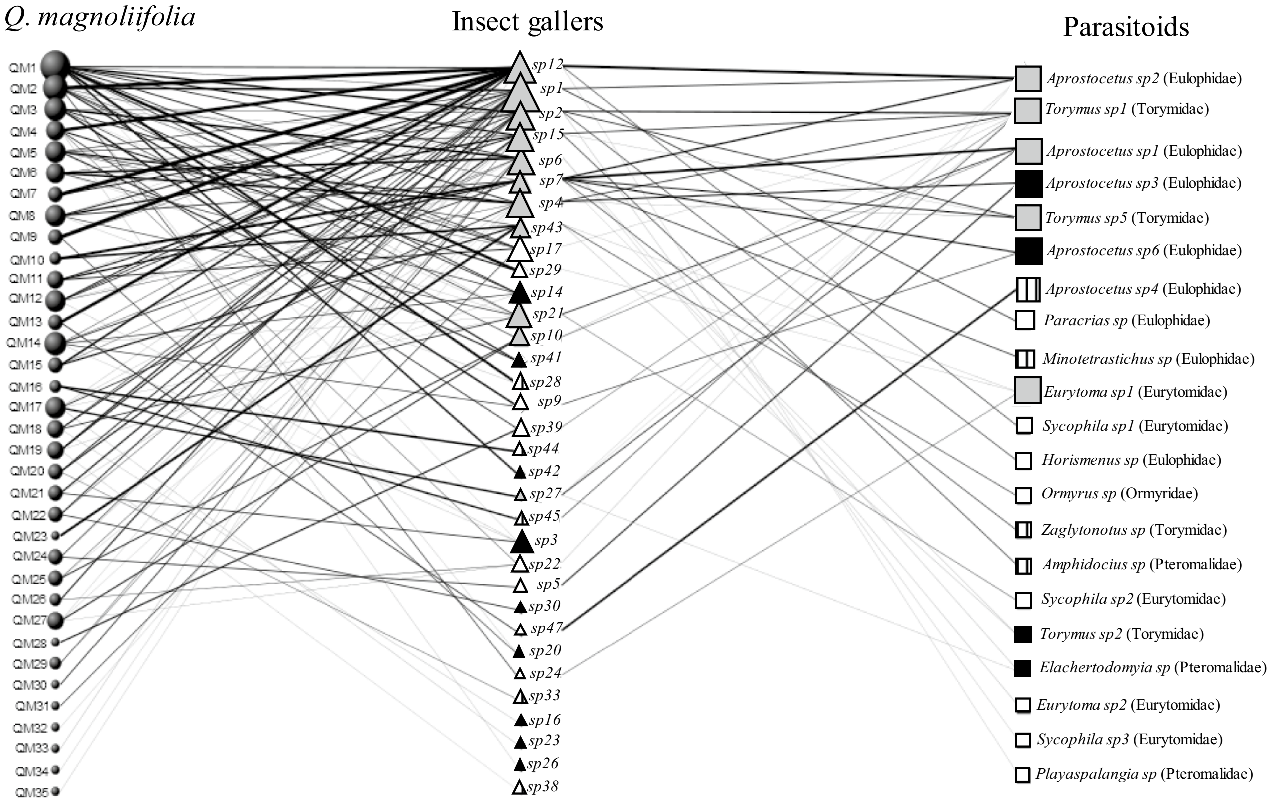

Fig. 2 Quantitative trophic network of *Q. magnoliifolia*. Line thickness represents the number of interactions (based on abundance). Insect galler morphospecies: Gray triangles: generalist species nucleus of insect gallers. White triangles: Insect gallers parasitized by a single parasitoid species. Black triangles: non-parasitized insect gallers. White triangles with lines: exclusive insect gallers to *Q. magnoliifolia*. Parasitoids: Gray squares: generalist species nucleus of parasitoids, White squares: Species that parasitized a single insect galler species (hyper-specialists). Black squares: Species that parasitized two insect galler species (specialists). White squares with lines: exclusive parasitoids to *Q. magnoliifolia*

respectively) and *Q. resinosa* (4.901, 10.3%, and 3.743, respectively) networks. On the other hand, the hybrid network had lower modularity (0.385) compared to *Q. magnoliifolia* (0.627) and *Q. resinosa* (0.462) networks. The value of specialization was high for *Q. magnoliifolia* (0.685) and low for hybrid (0.487) and *Q. resinosa* (0.479) networks. On the other hand, values of nestedness and vulnerability were higher for the *Q. resinosa* network (34.207 and 8.108, respectively) than for hybrid (20.902 and 3.863) and *Q. magnoliifolia* (16.154 and 2.525). Compared to null models, observed values of diversity of interactions, connectance, nestedness, generality, and vulnerability were lower than expected by chance for *Q. magnoliifolia*, *Q. resinosa*, and hybrid networks (Table 2). On the other hand, all insect galler-parasitoid networks have higher values of modularity and specialization than expected by null models.

Discussion

Most of the cynipid gall wasps are associated with the genus *Quercus* and include more than 1400 described species (Ronquist and Liljeblad 2001), representing the largest evolutionary group of the Hymenoptera (Cynipoidea), which is dominated by parasitoids. Although a general consensus has been reached that galls are plant tissues induced by insects that provide shelter, food of high nutritional quality, protection from both, environmental fluctuations and natural enemies such as parasitoids (Stone and Schönrogge 2003; Ronquist et al. 2015), little is known about the effects of plant hybridization on community assemblages of antagonistic trophic networks of insect gallers and their parasitoids (Pérez- Nakamura et al. 2010; López et al. 2016. Our findings are relevant

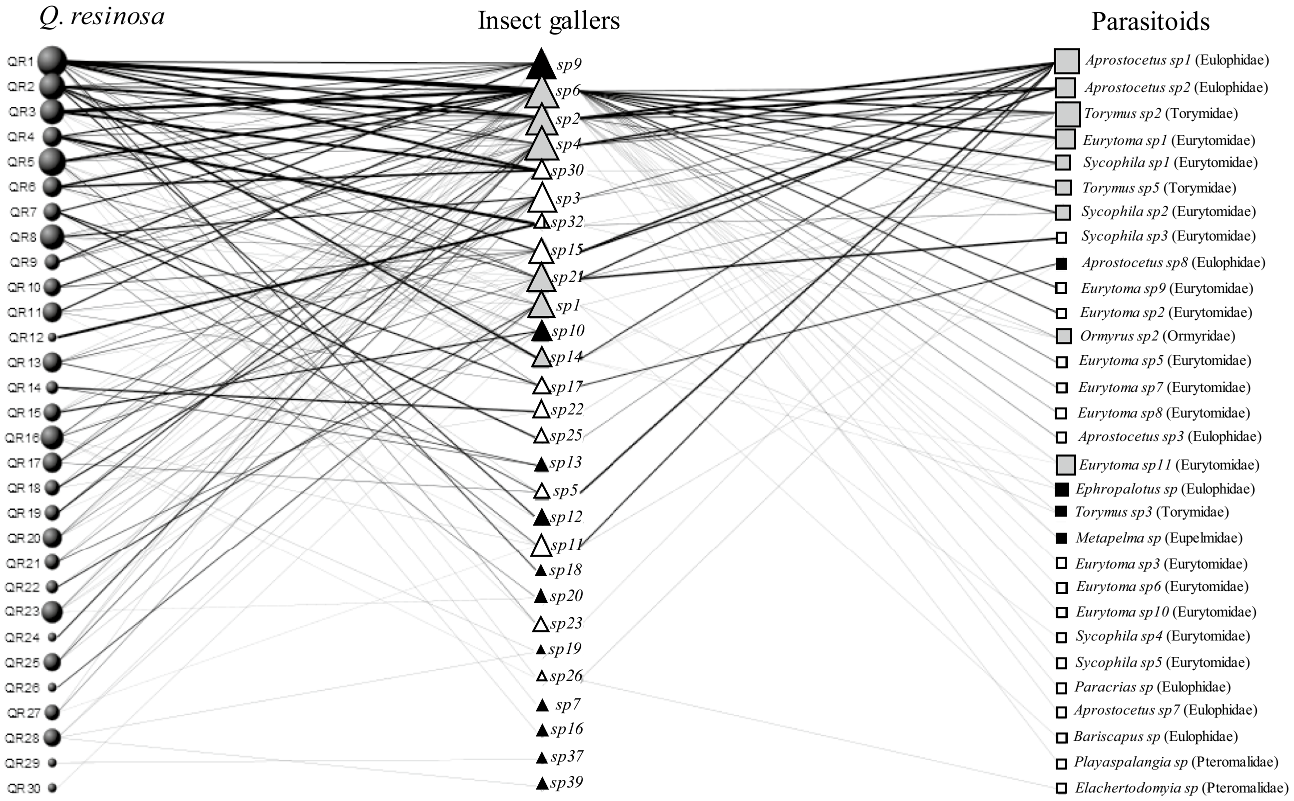

Fig. 3 Quantitative trophic network of *Q. resinosa.* Line thickness represents the number of interactions (based on abundance). Insect galler morphospecies: Gray triangles: generalist species nucleus of insect gallers. White triangles: Insect gallers parasitized by a single parasitoid species. Black triangles: non-parasitized insect gallers. White triangles with lines: exclusive insect gallers to *Q. resinosa.* Parasitoids: Gray squares: generalist species nucleus of parasitoids, White squares: Species that parasitized a single insect galler species (hyper-specialists). Black squares: Species that parasitized two insect galler species (specialists). White squares with lines: exclusive parasitoids to *Q. resinosa*

to understand the ecology and evolution of cynipid galler wasp assemblages on oak hybrid complexes, as well as the processes and mechanisms that shape and maintain insect diversity in the tree canopy of temperate species (Cuevas-Reyes et al. 2018).

In our study, according to genetic analyses, we identified three different oak groups that included individuals of *Q. magnoliifolia*, *Q. resinosa*, and hybrids. Regarding our fist research question, our results showed that insect galler communities, as well as parasitoid communities associated with them, were different among the three oak groups, suggesting that oak hybridization influences the tri-trophic networks in this oak hybrid complex at the Tequila Volcano. Particularly, plant–insect galler networks showed differences in the topological descriptors between *Q. magnoliifolia*, *Q. resinosa*, and hybrid networks, with the hybrid network having the highest diversity of interactions, as well as a greater nestedness and modularity than *Q. resinosa* and *Q. magnoliifolia* networks (see Table 1). A similar pattern was observed for the generality and vulnerability, these descriptors were higher for hybrid networks than for *Q. magnoliifolia* and *Q. resinosa* networks. These results suggest that hybrid oaks are more vulnerable to the occurrence of insect gallers (Pérez-López et al. 2016). This could be related to changes in genetic structure by the effect of the hybridization phenomenon (Rieseberg and Ellstrand 1993; Whitham et al. 1999; Cuevas-Reyes et al. 2018). Conversely, specialization (H2 index) was lower for hybrid networks in comparison with *Q. resinosa* and *Q. magnoliifolia* networks. This result indicates that different gall morphotypes are widely distributed among hybrid individuals, whereas, in parental plants, there is probably a segregation of morphotypes between different individuals.

Hybrid individuals represent a wide range of resources and conditions that can be exploited by their associated fauna (Fritz et al. 1999). This is due to increased resources, besides the high ecological and evolutionary activity that characterizes hybrid zones, as they may be generating new habitats for associated organisms (Tovar-Sánchez and Oyama 2006). Hybridization often results in new characteristics of the host plant, such as changes in foliar morphology (González-Rodríguez et al. 2004; Cuevas-Reyes

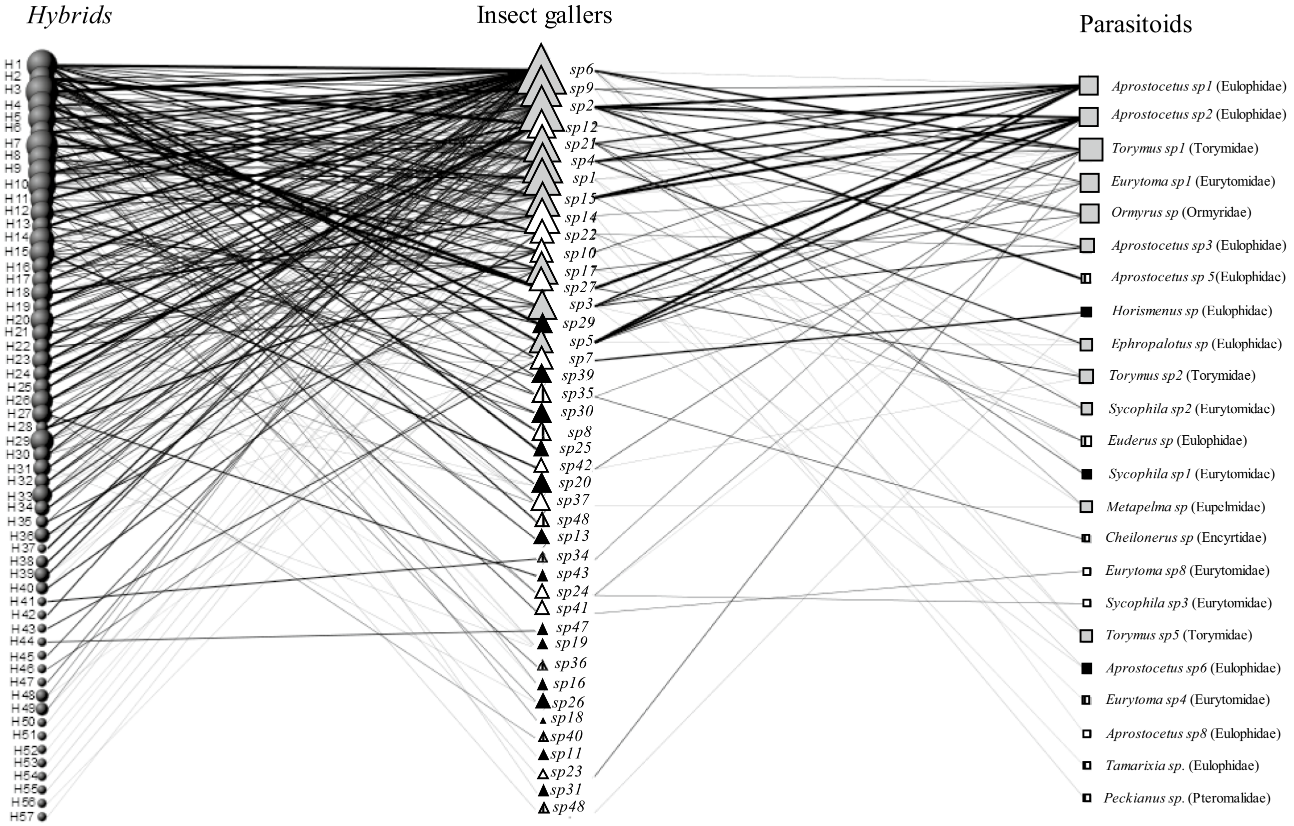

Fig. 4 Quantitative trophic network of *hybrids*. Line thickness represents the number of interactions (based on abundance). Insect galler morphospecies: Gray triangles: generalist species nucleus of insect gallers. White triangles: Insect gallers parasitized by a single parasitoid species. Black triangles: non-parasitized insect gallers. White triangles with lines: exclusive insect gallers to *hybrids*. Parasitoids: Gray squares: generalist species nucleus of parasitoids, White squares: Species that parasitized a single insect galler species (hyper-specialists). Black squares: Species that parasitized two insect galler species (specialists). White squares with lines: exclusive parasitoids to *hybrids*

Table 2 Descriptors of insect galler-parasitoid networks of *Q. magnoliifolia*, hybrids, and *Q. resinosa* oak individuals

Network descriptor	*Q. magnoliifolia*		Hybrids		*Q. resinosa*	
	Observed	Null models	Observed	Null models	Observed	Null models
Nsp-UTL	21	–	23	–	30	–
NSp-LTL	21	–	25	–	16	–
Diversity of interactions	3.324	4.560 (±0.017)	3.970	4.901 (±0.008)	3.920	4.717 (±0.014)
Connectance	0.104	0.351 (±0.008)	0.136	0.473 (±0.009)	0.103	0.307 (±0.007)
Nestedness	16.154	70.718 (±3.304)	20.902	78.678 (±2.173)	34.207	66.184 (±2.834)
Modularity	0.627	0.139 (±0.010)	0.385	0.086 (±0.006)	0.462	0.123 (±0.007)
Generality	3.315	10.169 (±1.336)	5.855	13.131 (±1.945)	3.743	7.115 (±3.000)
Vulnerability	2.525	7.616 (±1.337)	3.863	9.164 (±1.946)	8.108	13.164 (±3.006)
Specialization	0.685	0.086 (±0.008)	0.487	0.052 (±0.004)	0.479	0.071 (±0.007)

Number of species at the upper trophic level (Nsp-UTL). Number of species at the lower trophic level (NSp-LTL). All observed values were significantly different of null models ($P < 0.05$)

et al. 2018), phenology (Hunter et al. 1997), architecture (Bangert et al. 2005), as well as secondary chemistry (Cheng et al. 2011). These characteristics may be associated with the preferences of insect herbivores, their development and distribution (Fritz et al. 1999; Hochwender and Fritz 2004; Bailey et al. 2009).

Contrasting patterns with regard to the effect of hybridization on plants and their influence on the insect herbivore diversity have been found in several studies, ranging from higher, intermediate, lower, or even no difference in the composition of herbivores in hybrid plants (Fritz 1996; Floate et al. 2016; Pérez-López et al. 2016; Cuevas-Reyes et al. 2018). To explain these findings, a theory of the trophic level interactions has been proposed, predicting that the genotype of the plant can affect the susceptibility of herbivores to their natural enemies, because genetic recombination by hybridization effect can generate the rupture or dominance of the inheritable characters associated with the defense and/or establishment of herbivores in the host plant through different trophic levels (Fritz 1992; Fritz et al. 1996).

Networks composed by host plants and insect gallers tend to be highly specialized due to a large incidence of specialist insect species (Araújo and Maia 2021). Previous studies suggest that networks of cynipids tend to be more connected than networks of other groups of galling insects, due to the high level of overlapping interactions of insect gallers over *Quercus* species (Araújo et al. 2019). However, our results show that the structure of the interactions of cynipids and oaks is not homogeneous, but varies between different species and oak hybrids. On the other hand, the results of the connections of insect galler-parasitoid networks are within the range of previous studies on antagonistic networks, ranging from 10 to 16% of average interactions present in each subnet (Hirao and Murakami 2008; Kaartinen and Roslin 2012). Paniagua et al. (2009) suggest that greater connection is given by the number of parasitoid species associated with each gall-inducer (vulnerability) and not by the amplitude of the range of hosts (generality) presented by each parasitoid.

Regarding our second question, the interactions observed in the hybrid individuals between the insect gallers and parasitoids were more diverse, presenting greater generality in both oak-insect gallers and insect gallers-parasitoids subnetworks; while vulnerability was greater in hybrid plants only in the oak-insect galler subnetworks, and in the insect galling-parasitoid subnetwork the vulnerability was greater in *Q. resinosa*. These results point out that hybrid oaks are more vulnerable to the incidence of insect gallers, but in turn the insect gallers present in hybrids have lower pressure from natural enemies (parasitoids), which allow for the incidence of galls to be higher in hybrids. It has been well documented that parasitoid insects play a very important role in the trophic networks, because they influence density and population dynamics of their hosts (Hassell 2000).

In addition, insect gallers can differentiate between hybrid host plants from individuals of the parental species in hybrid zones of *Quercus* (Pérez-López et al. 2016), *Salix* (Hochwender and Fritz 2004), and *Populus* (Evans et al. 2012) as result of the recognition capacity of certain secondary metabolites associate to the host plants as well as the stimulation of injected fluids by female wasps during oviposition, or by secretions of saliva by larvae during feeding (Fritz et al. 2003). Other effects of these secondary metabolites are to act as feed deterrents for both herbivores (Lill and Marquis 2001) and natural enemies (Chaplin-Kramer et al. 2011). These results suggest that hybridization generates changes in the genetic structure of plants, which leads to fauna associated (i.e., insect gallers and their parasitoids) with such plant species to respond to inheritable plant characteristics (Crutsinger et al. 2006; Pérez-López et al. 2016) generating differences in the assembly of arthropods (Whitham et al. 2006; Underwood et al. 2009; Schädler et al. 2010), which confers a degree of resistance or susceptibility for herbivores (e.g., Fritz and Price, 1988; Dungey et al. 2000). These ideas agree with our study due the plant-galler networks of hybrids that were composed by 57 oak individuals and 42 insect galler species had the highest number of exclusive species of gall insects (16.6%), the highest diversity of interactions (5.583), nesting (30.468), and modularity (0.510) in comparison with *Q, magnoliifolia* and *Q. resinosa* networks.

With regard to the morphospecies of generalist nucleus insect gallers, differential patterns were observed between subnetworks. For the case of the oak-insect galler subnetworks, we find 13 to 15 generalist nucleus galls, of which nine are present in the subnetworks of the three species of oaks. This pattern of interaction where species of insect gallers categorized as a generalist nucleus co-occur with insect gallers that have fewer interactions with oak individuals, results in a nested topology, which indicates that the interactions recorded for oaks with a low incidence of insect gallers are a cohesive subset of the interactions found in oaks with a higher incidence of insect gallers. Therefore, these insect gallers are not a group of species that interacts with a specific group of oak individuals. Likewise, this nested topology allows the persistence of species of insect gallers minimizing the effect of inter-specific competition (Bastolla et al. 2009). While, in the insect galler-parasitoid subnetworks, the nested topology presents it only with the subnet of *Q. resinosa* individuals. The Jaccard similarity index showed that individuals of *Q. resinosa* and hybrids had the greatest similarity in the composition of insect gallers by 51% and parasitoids by 56%. This pattern could be related to those genetically more similar individuals, as it has been documented that plants with similar genotypes have a similar arthropod composition (Bangert 2006; Whitham et al. 2006; Floate et al. 2016).

Our study is one of the first to demonstrate how hybridization affects the structure of tri-trophic interactions between plants, insect gallers, and parasitoids show that plant hybridization generates differential patterns about the diversity of interactions between parental and hybrid plants with insect gallers and their parasitoids, where hybrid plants endure a greater diversity of interactions associated with the increase of genetic diversity. We postulate that hybrid plants are more vulnerable to the incidence of insect gallers and have low pressure by natural enemies (parasitoids), which allow higher occurrence of insect gallers on hybrid plants. In addition, is possible that the rupture or dominance of inheritable characteristics associated to the defense and/or establishment of insect herbivores on the host plant, gives insect gallers the ability to discriminate between hybrid and progenitor host plants, which can confer different degrees of resistance or susceptibility against insect gallers affecting upper trophic levels, such as parasitoids. This fact was confirmed, because the three-way network of hybrid individuals presented greater generatability of insect gallers and a lower vulnerability of parasitoids.

Acknowledgements The study was funded by Coordination of Scientific Research (UMSNH) project 005. This project was supported by CONACYT Project CB105755 and CONACYT PDC2016-Project-3053.

Author contributions YML, KO, and PCR: planned and designed the research. GPL MAZ, and PCR: conducted fieldwork. AGR, GPL, and KO: performed laboratory work. YML, WSA, MF, CDC, KSE, MAZ: conducted analyzed data. YML, WSA, AGR, KO, MF, KSE, MAZ, and PCR: The first draft of the manuscript was written. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability Data will be made available upon request.

Declarations

Conflicts of interest All authors declare that they have no conflict of interest.

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