



Foliar characteristics of neotropical forest affect assemblages structure of parasitoid insects

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Research Article

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Abstract

Several authors suggest that greater vegetation complexity provides more shelters, supporting higher parasitoid diversity. Additionally, it serves as visual cue in host searching. This study evaluates how visual stimuli and herbivore-induced vegetation changes affect parasitoid strategies and guilds in low deciduous forest [Yabucu], and Medium Semi-Evergreen forest [Noh-Bec]. We calculated the relative abundance of idiobiont and koinobiont life strategies for each vegetation type and constructed the range-abundance curves of these communities. Also, the relationship of guilds with the different types of damage from herbivory and leaf characteristics were described. The koinobiont:idiobiont (K:I) ratio was 6:1 (86.65% koinobionts and 13.35% idiobionts) in Yabucú and 1:2 (32.78% koinobionts and 67.22% idiobionts) in Noh-Bec. Some guilds were associated with vegetation: a negative correlation between fluctuating asymmetry seedlings (FAS) and parasitoids attacking larvae into the fruiting bodies of fungi was founded; the FAS is an indirect indicator of herbivory, nonetheless, the parasitoids found do not target phytophagous hosts, which makes an inverse relationship plausible and could potentially reduce intra-guild competition. Hyperparasitoids were positively associated with holes in adult plants (HA); with an association with herbivore parasitoids, which could be contributing to the recorded evidence of holes.

Introduction

Parasitoids are insects that grow inside or on the body of another arthropod, usually of phytophagous habits (Godfray 1994). Parasitoids follow two types of development strategies. The idiobiont strategy consists of inserting the ovipositor into the host body and injecting a poison that can paralyze, arrest its development, or kill it, and then lay an egg on its body so that the larva can feed on the host when it emerges. In the koinobiont strategy, the parasitoid allows the host to continue developing and growing after oviposition (Askew & Shaw 1986).

In both strategies, parasitoids have developed highly efficient search strategies and make decisions during the search for hosts at three levels (Cournoyer & Boivin 2004). First, they decide where to look for a host; second, where to focus their search; and, third, whether or not to lay an egg on/in the host once they have found it (Ueno & Ueno 2015). The first level involves the search for a vegetation patch within a landscape at great distances, responding both to volatile compounds emitted by plants and to visual signals derived from vegetation structure and composition of the habitat and the changes induced by the host in them (Sime 2004, Giunti et al. 2015). The second level consists of locating chemical and visual signals emitted by plants that have been attacked by herbivores (Castelo et al. 2010, Sime 2004).

In the third level, once the host is located, parasitoids use their antennae and ovipositor to assess whether the host is suitable for egg-laying, feeding, or both (Hughes et al. 1994). The structural complexity of the vegetation influences the search for both the patch and the host, regardless of the plant species richness (Zhang & Adams 2011). Some authors postulate that the greater the structural complexity of the vegetation, the higher the number of shelters available, which will allow to harbor a higher parasitoid diversity (Fraser et al. 2007, Hawkins 1988, Hawkins & Lawton 1987, Hawkins et al. 1992, Sääksjärvi et al. 2006). However, other authors claim that the volatile chemicals induced by herbivores feeding on different plant species can attract different species of parasitoids (Godfray 1994). Hence, structural complexity does not affect parasitoid diversity; instead, plant species composition is more important (Godfray 1994, Koricheva et al. 2000).

Considering this controversy and the little knowledge about the vegetation factors that might be influencing the first two parasitoid search levels, this work aims to determine the effect of vegetation structure on development strategies and guilds of the family Ichneumonidae that make up parasitoid communities in two types of tropical forest of the Yucatan Peninsula. To this

end, we assessed the visual stimuli and changes in herbivore-induced vegetation structural characteristics and their effect on the biological composition of parasitoid communities in different vegetation types in the Yucatan Peninsula, Mexico.

Materials and methods

Study area

We selected two sites of the Yucatan Peninsula corresponding to two different vegetation types. The first site, called **Yabucú** (latitude 20.810° and longitude -89.413°), is a Private Reserve located in the municipality of Acanceh, Yucatan, with altitudes between 0 m and 100 m a.s.l. It has a warm subhumid climate with summer rains. The annual temperature ranges between 26°C and 28°C, and the annual precipitation ranges from 1000 mm to 1100 mm. The site includes areas or patches of low deciduous forest (LDF) and secondary vegetation of different successional ages ranging from 5, 8, 10, 15, and 20 years (Flores-Guido & Espejel-Carvajal, 1994).

The other site, called **Noh Bec** (latitude 19.143056° and longitude -88.169167°), is located in the center of Quintana Roo State in the municipality of Felipe Carrillo Puerto, Yucatan Peninsula, Mexico. It is part of the corridor linking the Sian ka'an and Calakmul Biosphere Reserves. It comprises a territory of 24,122 hectares with patches of Medium Semi-Evergreen Forest (MSEF) and an area of Permanent Forest Area of 18 thousand hectares for logging.

In addition, it includes an Ejidal Forest Reserve called El Huasteco, comprising an area of 700 hectares for wildlife protection and conservation. Noh Bec is a forest community organized in three major sectors: the Noh Bec Ejido that manages forest resources; Noh Bec S.P.R. (Productos de Bosques Tropicales Certificados Noh Bec, S.P.R. de R.L.), a major stake-holder in industrial development, and the Noh Bec Gum Cooperative, in charge of gum collection.

Field sampling of parasitoids

Ichneumonids were sampled using Malaise traps, which are extensively used in parasitoid monitoring programs (Fraser et al. 2007, Chan-Canché et al. 2020). In each of the two sites (LDF, MSEF), ten traps were placed in the center of the vegetation patch, forming a square with the traps placed at a regular distance from each other. These traps operated uninterruptedly during five months (June–October) in the rainy season, with collecting jars replaced every 15 days.

The samples collected in the field were sent to the Instituto Tecnológico de Conkal, where specimens were sorted according to taxonomic groups, mounted and identified taxonomically for a correct characterization of the parasitoid guilds.

Guilds' definition

Parasitoid species were classified in the following guilds (Mazón and Bordera 2014):

gPh, those attacking exposed phytophagous larvae feeding on external parts of plants, such as leaves, stems, flowers, and buds.

Sap, parasitoids of saprophagous larvae.

Hyp, hyperparasitoids, whose host range includes many species of primary parasitoids.

Coc, parasitoids of cocoons and pupae.

Myc, parasitoids of larvae found in the fruiting bodies of mushrooms and bracket fungi.

Xyl, parasitoids of xylophagous larvae, excluding those feeding on dead but not decomposing wood.

Mel, parasitoids of melitophagous larvae of bees that feed on stores of honeydew, nectar, and pollen, and of wasp larvae living in nests.

Poly, parasitoids whose host range includes two or more arthropod orders with different trophic habits.

Zoo, parasitoids of zoophagous larvae and spiders.

Unkn, parasitoids whose hosts are unknown.

Vegetation sampling

Ten circles of 10 meters in radius (20 m diameter) were delimited in each vegetation type, considering the Malaise trap as the center; each circle was divided into four identical sections (Figure 1). One such section was selected for manual leaf collection (sampling one-quarter of the circle per month until completing the circle at the end of the sampling, and then alternating the direction of each quarter to cover the four cardinal points). Ten leaves were collected from each individual plant, considering the following criteria: for plants with a height <1.5 m (including seedlings), five leaves were collected from the outer part of the canopy and five from the inner part (three leaves in the case of seedlings).

Herbivory and leaf characteristics

The types of foliar herbivory were determined (Table 1) according to the methodology proposed by Crawley (1983), as well as the frequency of each type by leaf and by collection circle (Malaise). Besides, the leaf characteristics of each plant were measured (differentiating between adults and seedlings): hardness and thickness, side length, fluctuating asymmetry, total leaf area, and missing leaf area, using the ImageJ software. The environmental variables relative humidity and temperature were measured in each collection circle during the five months of sampling.

Data analysis

We described the Ichneumonidae assemblages in each vegetation type, determining the composition of guilds and the proportion of development strategies (koinobiont and idiobiont). The community structure was described by constructing rank-abundance curves and development strategies of guild communities (also known as Whittaker curves) were constructed (Magurran 2004).

The influence of vegetation structure on development strategies (regulating the way in which guild assemblages interact) was established by determining the visual signals derived from vegetation structure (frequency of damage by herbivory of potential hosts) that influence the establishment of populations of this family of parasitoid wasps.

Partial linear correlation analyses were performed using the PAST statistical software (Hammer et al. 2001), to determine whether there are significant relationships between leaf characteristics, type of herbivory damage, and the biological composition of ichneumonid assemblages (guilds) in the two vegetation types. Significant correlations ($P < 0.05$) among parasitoid guild abundance are given in the form of a correlation matrix, while significant correlations between guild abundances and all the other variables are represented as correlation networks. Guilds with less than 20 individuals were not used for the analysis.

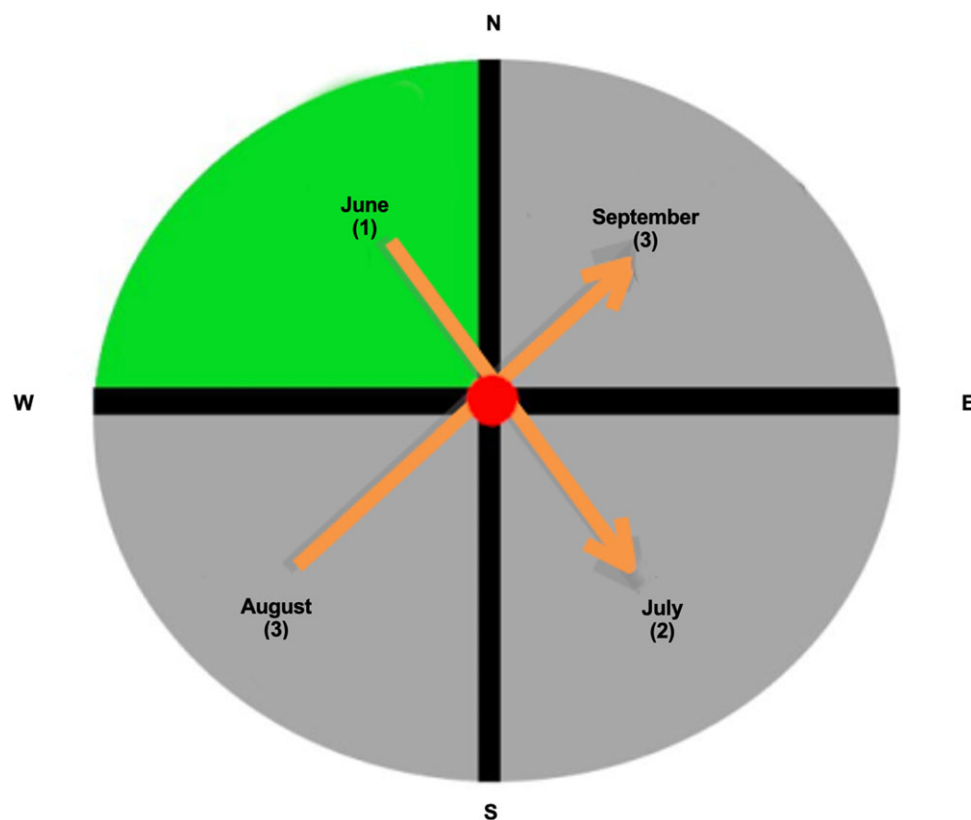


Figure 1. Diagram indicating the vegetation sampling area (filled in green). The red spot corresponding to Malaise trap.

Results

Development strategies and composition of ichneumonid assemblages

A total of 1699 individuals belonging to 168 morpho-species of the family Ichneumonidae were collected, of which 59.86% are parasitoids with a koinobiont strategy (1017 individuals) and 40.14% with a idiobiont strategy (682 individuals) (Table 2). We found differences by site in the koinobionts/idiobionts (K:I) ratio: LDF showed a 6:1 ratio, 746 koinobionts (86.65%) and 114 idiobionts (13.35%), while MSEF displayed a shift in the dominant strategy, with a 1:2 ratio, 277 koinobionts (32.78%) and 568 idiobionts (67.22%). Both strategies were represented by 11 parasitoid guilds, with no significant differences in the abundance between sites (50.26% collected in Yabucú and 49.74% in Noh Bec) (Table 3).

Koinobionts were more abundant in the LDF, with *gPh* and *cPh* as the best-represented guilds; idiobionts showed a reduced guild composition, *Unkn* and *Coc* being the only guilds observed (Figure 2). By contrast, in idiobionts were more abundant in the MSEF; however, as in the LDF, koinobionts showed more heterogeneous communities than idiobionts. This suggests that sites with more complex tropical vegetation (MSEF) simultaneously host a large number of specialist (koinobiontes) and generalist (idiobiontes) taxa (Figure 2).

When comparing the composition of koinobiont assemblages collected in the two vegetation types (LDF and MSEF), the slope of the curve found in the LDF reflects less even — and, therefore, less diverse — assemblages than in Noh Bec, with *gPh* and *cPh* being the dominant guilds. For its part, in the MSEF there was no marked dominance, but the most abundant guild was *cPh* (Figure 2). In the case of the composition of idiobiont ichneumonid assemblages

collected in the two vegetation types (LDF and MSEF), the highest guild richness was observed in the MSEF of Noh Bec, with *Unkn* and *Coc* being the most abundant guilds; this contrasts with the Yabucú LDF, where only 2 guilds were found (Figure 2).

Influence of foliar characteristics and herbivory on the establishment of guilds

In Table 4 is given the partial correlation coefficients among parasitoids guild's abundances, it is noteworthy that some of them are highly correlated (i.e. the absolute value of partial r is close to 1), indicating that many of them could be driven by the same environmental factors.

There were only two guilds which abundances were correlated with vegetation or herbivory variables; *Hyp*, which was positively correlated to holes in adults, and *Myc* which was negatively correlated to FAS, Fluctuating Asymmetry Seedlings, although this partial correlation was marginally significant ($P = 0.06$). In Figure 3, the correlation networks among these guilds and other variables are shown.

Discussion

Development strategies and composition of ichneumonid assemblages

The observed differences in the proportions of koinobionts and idiobionts between the two localities can be explained because the vegetation structure represented in the LDF is less complex. Consequently, the predominant development strategy in the biological composition of Ichneumonidae assemblages consists of highly specialized parasitoids that attack specific hosts associated

Table 1. Types of foliar herbivory (Crawley 1983)

Type of damage	Characteristic
Cut-outs	Damage generally on the margins and edges of the leaves.
Holes	Damage to the leaves in the form of a continuous hole in the leaf.
Windows	Damage to the leaves, but with the rest of the individual cell layer intact.
Scraping	Elimination of the layer of cells from the surface of the leaf.
Mines	Continuous mine damage on the leaves, visible from both sides.
Skeletonization	Damage caused by holes in the leaves along the veins of the leaf.

Table 2. Abundance of each development strategy at each site

Site	Koinobionts	Idiobionts	Total
Noh-Bec	277	568	845
Yabucú	740	114	854
Total	1017	682	1699

with a certain plant composition: koinobiosis (Sheenan & Hawkins 1991).

These results seem to contradict the host predation hypothesis (Rathcke & Price 1976), the parasitoid predation hypothesis (Gauld 1988), and the resource fragmentation hypothesis (Janzen 1981). In the first two cases, as a result of stronger selective pressures by predators on specialist koinobionts taxa, and in the third, due to the supposed low host density, a higher abundance of generalist idiobionts is predicted in sites with tropical vegetation (Borer *et al.* 2012). However, since the abundance and diversity of koinobiont guilds in Yabucú are higher than those of idiobionts, the results indicate that the disturbed and non-diverse LDF is capable of hosting a wide range of specialist taxa.

A more comprehensive interpretation of the resource fragmentation hypothesis (Janzen 1981) indicates that the low host density in the Yabucú LDF probably acts by selecting koinobionts that are extremely efficient in locating scattered hosts. In addition, most koinobionts are endoparasitoids, that is, they oviposit inside the eggs or early-stage larvae of their hosts (Shaw & Huddleston 1991). Therefore, they are more likely to be successful in environments with higher abiotic stress, such as LDF, where insolation is higher than in the MSEF.

On the other hand, a higher abundance of idiobionts was found in the Noh Bec MSEF, being *Unkn* and *Coc* the dominant guilds. By contrast, koinobionts formed more even assemblages in terms of abundance, with *cPh* being the most abundant guild (Figure 4). This may be due to the fact that the most complex and diverse vegetation has a greater number of plant species and, according to the enemy hypothesis (Root 1973), it is predictive of a higher diversity of herbivores and, therefore, a wider range of hosts than simpler vegetation structures. The above is consistent with idiobionts being mostly ectoparasitoids

Table 3. Guild abundance in two tropical forest

Guild	Noh-Bec MSEF	Yabucú LDF	Total
<i>gPh</i>	25	399	424
<i>cPh</i>	135	228	364
<i>Sap</i>	6	2	8
<i>Hyp</i>	4	14	18
<i>Coc</i>	103	42	145
<i>Myc</i>	46	34	80
<i>Xyl</i>	4	1	5
<i>Mel</i>	1	0	1
<i>Poly</i>	0	0	0
<i>Zoo</i>	0	0	0
<i>Unkn</i>	521	134	655
Total	845	854	1699

Table 4. Partial correlation coefficients among guilds' abundances, all *P* values were < 0.05

Guild	<i>gPh</i>	<i>cPh</i>	<i>Hyp</i>	<i>Coc</i>	<i>Myc</i>	<i>Unkn</i>	K
<i>cPh</i>	-1	—	—	—	—	—	—
<i>Hyp</i>	-0.48	-0.49	—	—	—	—	—
<i>Coc</i>	-0.89	-0.9	-0.45	—	—	—	—
<i>Myc</i>	-0.93	-0.93	-0.42	-0.83	—	—	—
<i>Unkn</i>	-0.94	-0.95	-0.53	-0.92	-0.87	—	—
K	1	1	0.51	0.9	0.94	0.95	—
I	0.93	0.94	0.54	0.94	0.87	1	-0.95

and generalists (Shaw & Huddleston 1991), so they can be favored in forests with greater vegetation structural complexity. Likewise, this could be explained based on the theory of host predation (Rathcke & Price 1976), which predicts that parasitized herbivores will be subjected to heavier predation than healthy individuals. Therefore, parasitoids would display higher juvenile mortality rates, leading to a larger number of parasitoids exploiting hosts less susceptible to predation (e.g. pupae) or hosts that hide and are protected by plant parts, as do many idiobiont taxa.

An additional explanation (not mutually exclusive with the above) becomes evident when observing that the most abundant idiobiont guild in both sites is *Unkn*, suggesting that although idiobionts are well-represented, there is little knowledge about their taxonomy and biology in tropical regions (Veijalainen *et al.* 2012), both in the Yabucú LDF and in the Noh Bec MSEF. Likewise, when observing the koinobiont guilds in both sites, it becomes evident that *Unkn* is among the dominant guilds. This indicates the enormous knowledge gap about the guilds of Ichneumonidae parasitoids in tropical regions. It is necessary to carry out more studies relating the parasitoid biology with vegetation, climate and host species, which will help us to understand the observed patterns.

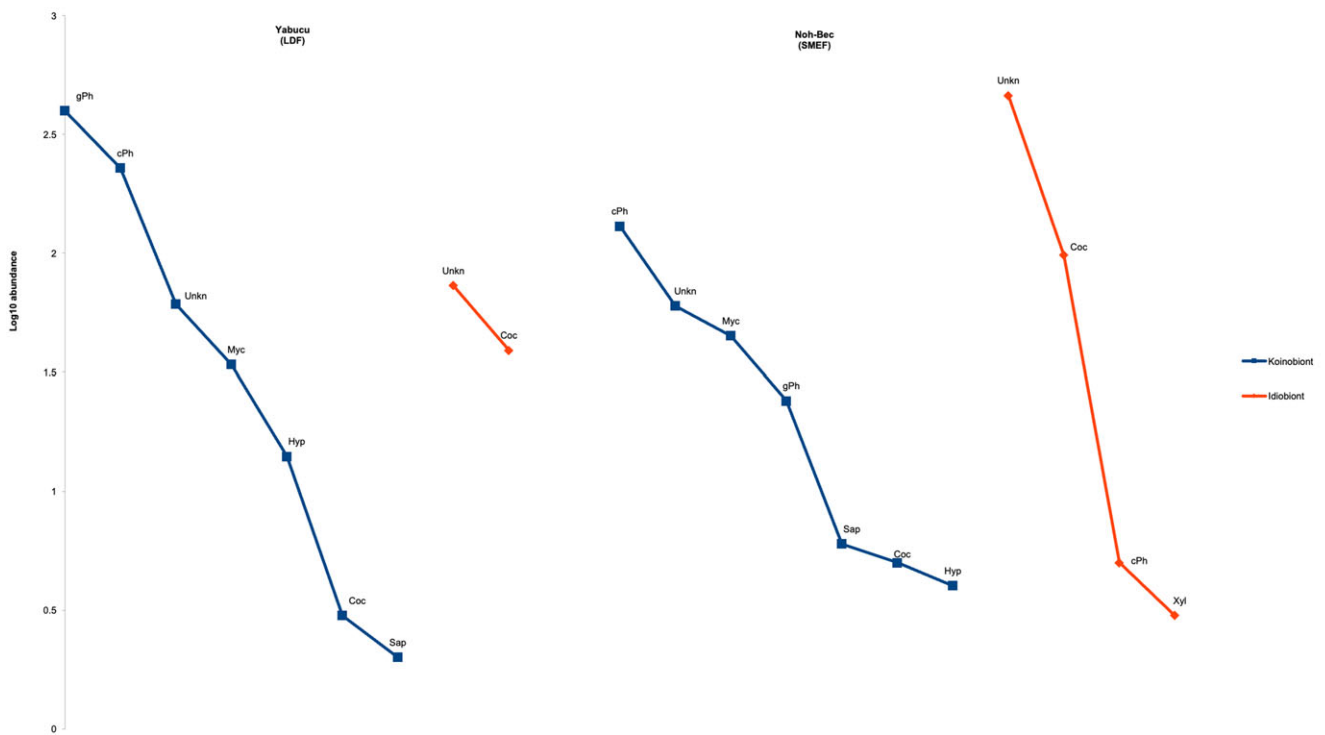


Figure 2. Rank–abundance plots of ichneumonid guilds ensembles collected from LDF and SMEF. A logarithmic scale of abundance was plotted against the species-rank ordered by guilds, from those with the most abundant individuals to those with the fewest.

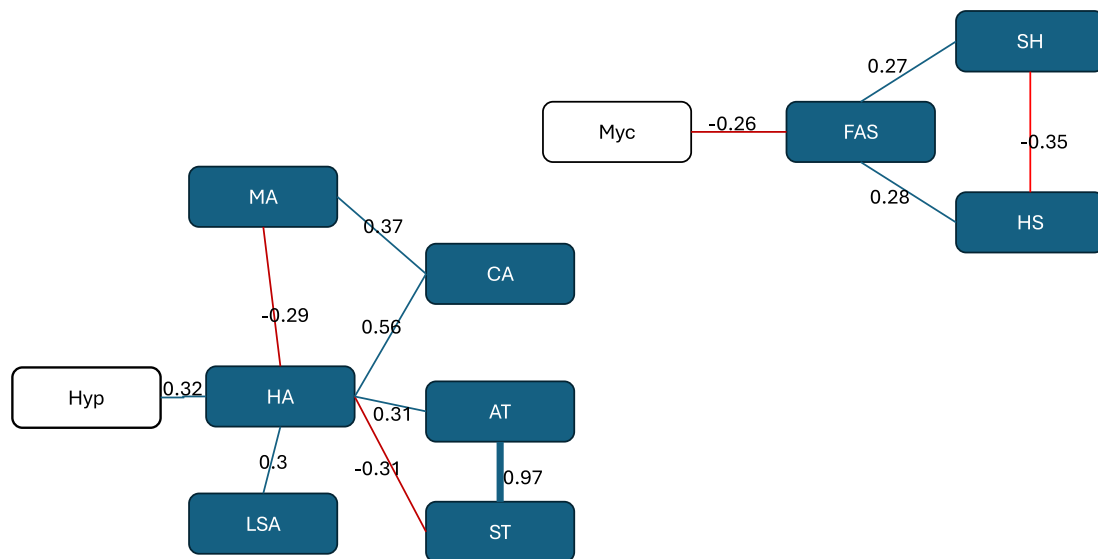


Figure 3. Correlation networks between guilds' abundances (in orange rectangles) and the other variables (in blue rectangles). Blue links are positive correlations, while red ones are negative. Link between Adult Thickness (A.T) and Seedling Thickness (S.T.), is represented thicker for stressing the strong direct correlation. All *P* were < 0.05, except for *Myc* with AFP, with *P* = 0.065.

Influence of foliar characteristics and herbivory on the establishment of guilds

It was observed that seedling fluctuating asymmetry (FAS) increased with holes in leaves of seedlings and adult plants (HS and HA respectively). It is noteworthy that it has been reported that tropical tree species with higher herbivory presented higher fluctuating asymmetry level (Cuevas-Reyes et al. 2013). The

fluctuating asymmetry (FAS) is an indirect indicator of herbivory, which tends to be higher in the low deciduous forest (Yabucú); fungi are also scarcer in this dryer forest, which in turn leads to lower abundances of the organisms related to this energy channel. This may explain the negative correlation between FAS and *Myc* (parasitoids attacking larvae found the fruiting bodies of mushrooms).

All hyperparasitoids (*Hyp*) belonged to the family Mesochorinae, and were positively associated with holes in adult plants (HA). The host species of this family, which are in turn parasitoids of herbivores, are strongly associated with vegetation structure and herbivores abundance, which may be indirectly indicated by HA.

Conclusion

Herbivory-induced changes in vegetation structure favor and are key factors in the establishment of guilds and development strategies of the Ichneumonidae. Studying them offers a supplementary tool to efficiently characterize and describe the composition of these parasitoid assemblages, especially in tropical regions with LDF and MSEF.

We found that a herbivory indicator such as holes in leaves of adults (HA) is correlated to hyperparasitoid abundance, which is in turn significantly correlated to several other parasitoid guilds, this is expected as more herbivore may be indicating larger populations of herbivores, as well as of their enemies, some of which are the host species of the hyperparasitoids.

We also found a negative correlation among fluctuating asymmetry (FAS) and the parasitoids feeding on the larvae which live in mushrooms; this could be explained as FAS is higher in the dryer forest, in which fungi are not as abundant, affecting the rest of the trophic chain depending on them.

The distribution of development strategies of Ichneumonidae observed in this study follows a clear pattern: specialist koinobionts are associated with LDF (Yabucú) and generalist idiobionts are mainly associated with the site with MSEF (Noh Bec). However, the fact that the parasitoid guild whose hosts are unknown (*Unkn*) is among the dominant guilds in both sites and development strategies suggests that any anomalies in the latitudinal distribution of tropical Ichneumonidae are likely artifacts resulting from biased sampling methods leading to underestimating the true diversity of this family in the tropics, particularly in the case of small koinobionts.

Future studies should include experimental designs (supplementing traditional sampling methods) to determine and evaluate the impact of the set of auditory, visual, and chemical stimuli unrelated to vegetation, such as odor traces emitted by potential hosts and other parasitoids. Also, it is important to note that this study only covers the patterns associated to the rainy season, so studies in different seasons are necessary for understanding further the ecology of parasitoids and preys.

Since parasitoids play a central role in multitrophic interactions, underestimating the diversity of tropical Ichneumonidae challenges not only any conclusions about latitudinal trends in the family, but also any conclusion about the level of impact of ichneumonid species on the tropical ecosystem dynamics in the Yucatan Peninsula.

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Competing interests. The authors declare none.

Ethical statement. None.

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